Ficus Subgen. Ficus. Two Rare and Primitive Pachycaul Species

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FICUS SUBGEN. *FICUS*. TWO RARE AND PRIMITIVE PACHYCAUL SPECIES

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CONTENTS

Ficus diamantiphylla (sect. *Ficus* ser. *Auratae* Corner) is described as a new species from Borneo, *F. sciaphila* (sect. *Sycidium* Miq. ser. *Copiosae* Corner) as a new species from New Britain. Both are small pachycaul trees of limited distribution presenting the most primitive vegetative and floral characters in their series. They contrast with the leptocaul species which, with advanced structure, become the common and widespread members of the series. Both species illustrate the manner in which subgeneric evolution, origin and dispersal can be learnt from the pachycaul-leptocaul sequence. *F. diamantiphylla* places the origin of ser. *Auratae* in Borneo where the series is mainly endemic. It links with the widespread ser. *Eriosyceae* Corner, and it is shown how subsect. *Eriosycea* (Miq.) Corner bears upon the Sino-Himalayan origin of ser. *Cariceae* Corner with *F. carica* L. Specific evolution involves the production of new growth-forms and the occupation of new habitats; vicariism plays so little, if any, part that primitive and advanced species live in the same forest. *F. sciaphila* places the origin of ser. *Copiosae*, so far as the species with smooth seeds is concerned, in Melanesia in close proximity with ser. *Phaeopilosae* Corner and ser. *Scabrae* Miq. It is the pachycaul antecedent to the common and widespread *F. copiosa* Steud. and *F. wassa* Roxb.

Introduction

In recent years there have come into my hands two undescribed pachycaul species of *Ficus*, one from Borneo, the other from New Britain. They illustrate the thesis that in a large genus of flowering plants the derivation, evolution and dispersal of subgeneric groups need to be read from the pachycaul element. Each of the new species locates the source of a well-known series in which the leptocaul species are widely distributed, often collected, ecologically important in secondary and man-made habitats, and frequently noted in ethnobotanical surveys. Both species are clearly rare; I can affirm the point for *F. sciaphila* (ser. *Copiosae*) from my own search for it in New Britain. I use them, therefore, as ancestral relics in continuation of the argument within

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the detail of *Ficus* though, as I have repeatedly emphasized, the pachycaul-leptocaul manner of evolution is by no means the peculiarity of this one genus. The view is still prevalent, however, among those familiar rather with the advanced leptocaul vegetation of temperate floras than with tree evolution in the tropics that the pachycaul species are modern successes of exotic climates. Thus much evolutionary thought about angiosperms is inverted and, through this fundamental misconception, progress is paralysed.

I. *F. diamantiphylla* sp.nov. in sect. *Ficus* subsect. *Eriosycea* ser. *Auratae*

Subsect. *Eriosycea*

In the dioecious subgen. *Ficus*, the character of sect. *Ficus* lies in the non-climbing habit, the bistaminate male flowers with free filaments and the more or less free segments of the perianth. Critical details are given in my check-list (Corner 1965, pp. 116–118). The 30 species of subsect. *Eriosycea* are narrowly yet well distinguished by three, seemingly trivial, characters. The leaves lack cystoliths and appear, then, not to belong to *Ficus*. The seeds are coarsely tuberculate and have, mostly, a double basal keel, but they are not so compressed as in sect. *Adenosperma*. Lastly, the lignified wall of this seed (endocarp of the pyrene) has external to a few layers of tangentially arranged sclerotic cells a layer of narrow, radially elongate, almost prismatic cells, the varying lengths of which make the tubercles on the seeds (figure 4). These points define a close alliance of shrubs and trees distributed mainly round the China Sea, but ranging from Nepal and Sumatra to Timor and New Guinea; about half the species occur in Borneo. Additional features are the densely hairy twigs and leaves of many species and the palmately lobed, often cordate and dentate, membranous lamina of large size and with abundant transverse intercostal venation. Thus, in habit, subsect. *Eriosycea* is the group that resembles most closely the cultivated fig *F. carica* (smooth seeds, abundant cystoliths); and the origin of ser. *Cariceae* (*F. carica*, *F. palmata*, and *F. iidaiana*) is bound up with that of subsect. *Eriosycea*.

I have recognized two series and six subseries (Corner 1960*a*, 1965). There are, however, some little known species which render the classification uncertain. Both series (*Auratae*, *Eriosyceae*) display in four of the subseries pachycaul-leptocaul evolution and have produced in parallel both fairly tall trees (intermediate between pachycaul and leptocaul states) and more or less glabrous species with much simplified, even lanceolate, leaf. The tall trees are *F. tricolor* (20 m, subser. *Eriosyceae*), *F. halmaherae* (30 m, subser. *Trichosyceae*), *F. glandulifera* and *F. lamponga* (30 and 18 m respectively, subser. *Dehiscentes*), and *F. endospermifolia* (25 m, subser. *Auratae*). Another parallel has been the evolution of small-leafed mountain shrubs or treelets in subser. *Cuneifolieae* (*F. litseifolia*, *F. oreophila*) and subser. *Monandreae* (*F. macilenta*, *F. setiflora*); they are comparable with the montane variations of *F. oleaefolia* (Corner 1969*a*).

The leaves, whether large (30–50 cm long) or small (4–10 cm) are built up from comparatively little apical growth. A short tip with few vestigial veins surmounts a lamina with 4–6 pairs of lateral veins. In large leaves the lateral veins are widely spaced by intercalary growth with numerous transverse intercostals. The main region of this growth lies between the principal basal veins and the first pair of lateral veins. The basal veins extend, accordingly, for one-third to two-thirds of the length of the lamina and express in this manner the webbing of the palmatifid form into the cordate base. In a sense these are basipetally developed leaves with as much basal expansion as elongation. Leptocaul species with small leaves have reduced intercalary growth, fewer intercostals, narrower and often cuneate base, and more or less entire margin. In several species, as *F. grossularioides* (figure 1), *F. brunneo-aurata* (figure 6) or *F. hirta*

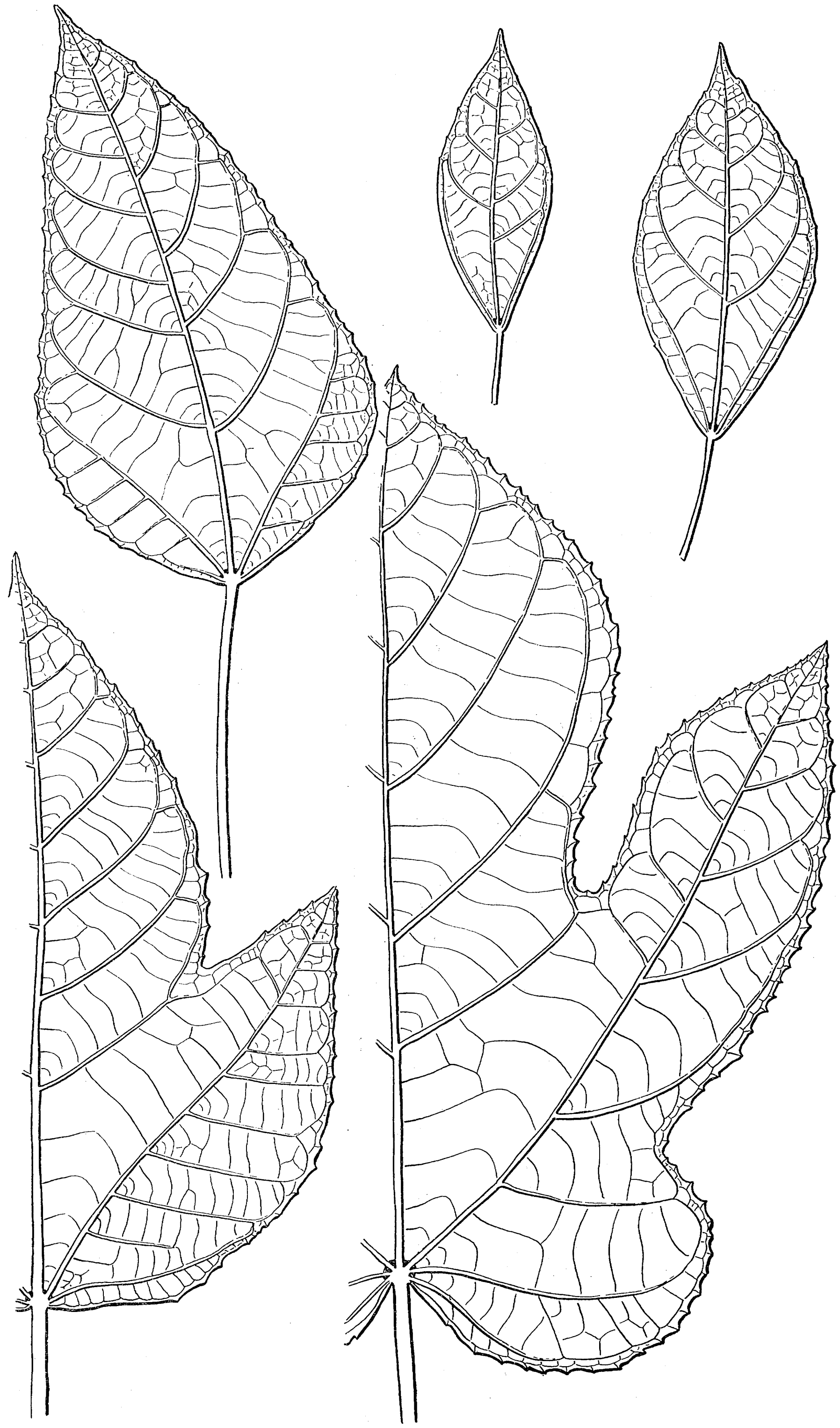

FIGURE 1. *F. grossularioides*, sapling leaf (palmately lobed), adult leaves (simple with cuneate base) and intermediate leaves, × ½.

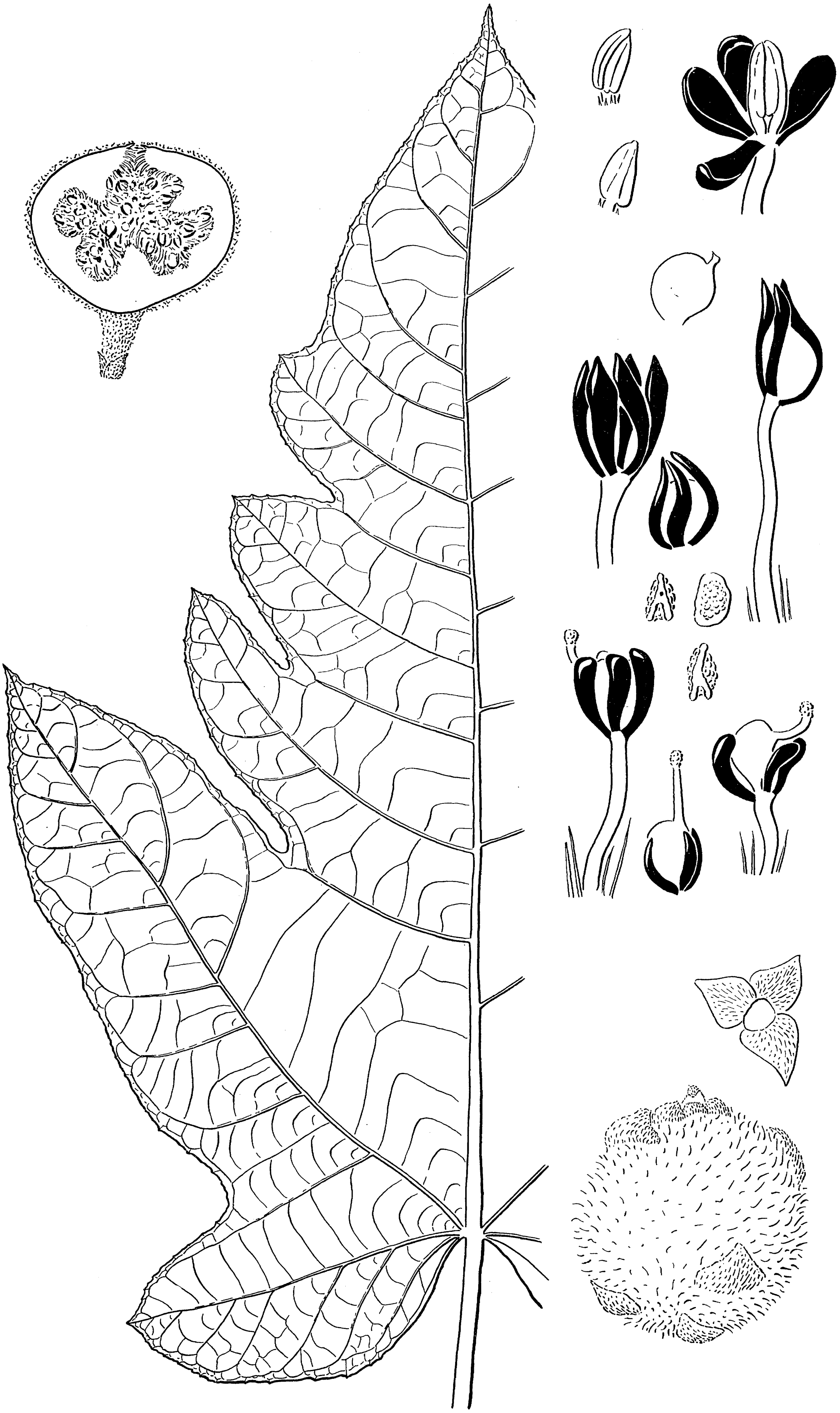

FIGURE 2. *F. padana*, sapling leaf, ×$\frac{1}{2}$, Junghuhn n. 1; fig, ×1; flowers and seeds, ×10, Back. v.d. Brink 7383 and S.F.n. 7275. *F. hirta* var. *squamosa* (lower right), fig, ×2, Hagerup s.n. 25 Nov. 1916.

(Hill 1967), the transition from the large palmatifid leaf to the lanceolate elliptic leaf can be followed on the same plant from sapling to old age. The vigorous growth of *F. grossularioides* peters out when the buds reach a height of 6–12 m; the leaves have 12–16 pairs of lateral veins, of which 6–9 develop intercostal areas in the sapling and 4–6 in the adult. In *F. padana* (figure 2), with the same number of lateral veins, the sapling leaf is not only palmatifid but pinnately lobed along the extended mid-lobe, as may happen in some forms of *F. carica*. As this mid-lobe shortens with less intercalary development, so its pinnate lobing diminishes (*F. fulva*, figure 3) and leads to the state which is merely palmately lobed. Then, as the leptocaul condition prevails from seedling to adult, the palmate lobing decreases (*F. chartacea*, figure 17) and may be lost entirely as seems to be the case in *F. litseifolia*, *F. oreophila*, *F. tuphapensis* and *F. langkokensis*

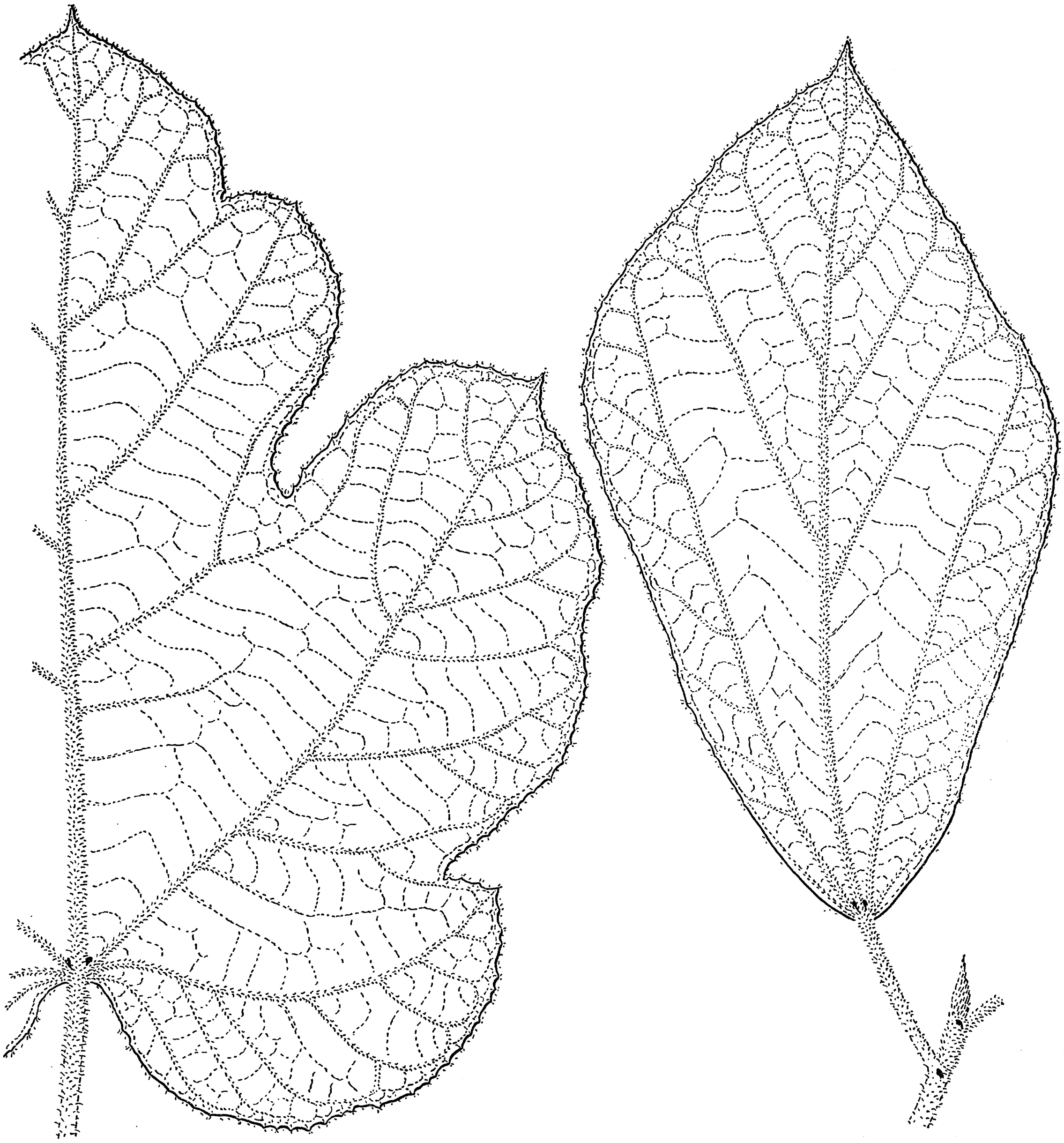

FIGURE 3. *F. fulva* from Java; sapling leaf (Thorenaar 116) and adult leaf with extended basal veins (Koorders 14291), × ½.

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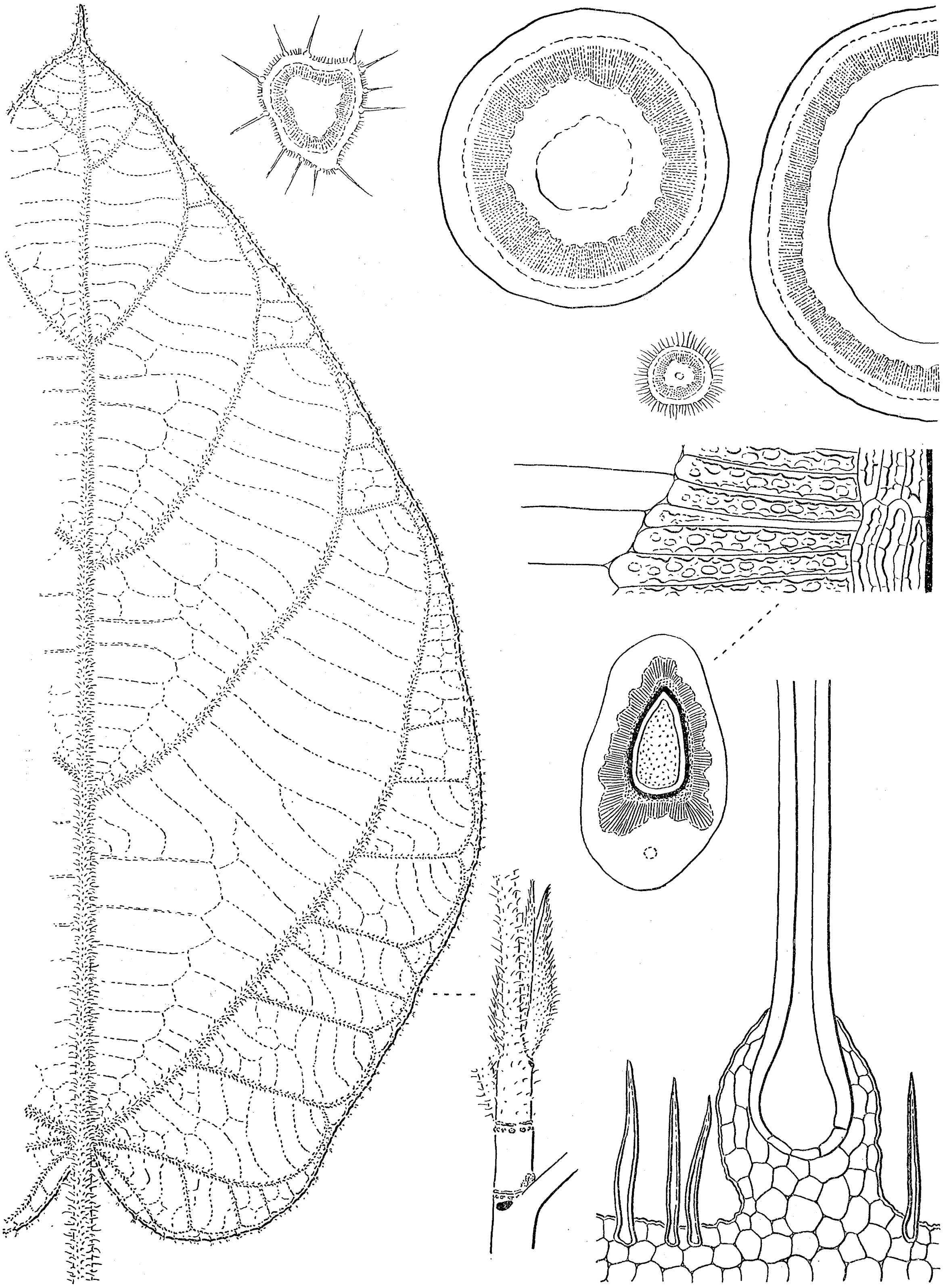

FIGURE 4. *F. bruneiensis*, leaf and twig (S. 19870), × ½. Sections of the twigs (taken above the third open leaf from the apex) of *F. bruneiensis* (upper right), *F. endospermifolia* (centre) *F. aurata* (upper left) and *F. setiflora* (small twig), × 5. Section of the fruit (× 25) of *F. endospermifolia* and the microscopic structure of the endocarp (× 500). Double indumentum of *F. brunneo-aurata* with basally supported long hair, × 220.

(figures 18 to 20). Whether there is any palmate lobing in subser. *Dehiscentes* (*F. ruficaulis*, *F. glandulifera*, *F. lamponga*) with entire leaf has yet to be ascertained; saplings of these plants are seldom collected or noted, for they are sterile and ecologists have not begun to consider them, but I came across a sapling with 3–5 palmately lobed leaf once in Johore which seemed to

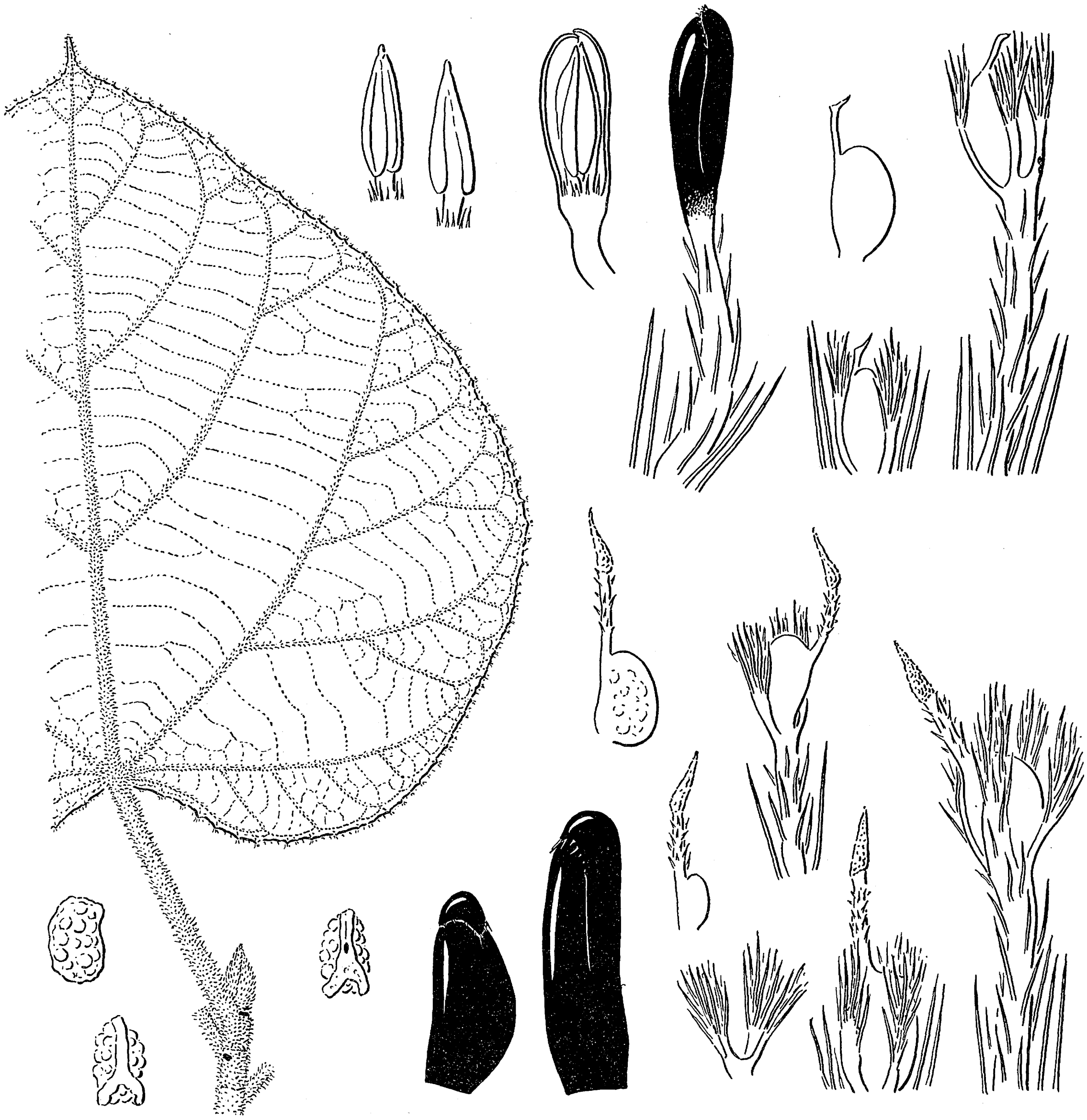

FIGURE 5. *F. endospermifolia*, leaf, × ½, S.F.n. 27842; male and gall-flowers, × 10, Clemens 3438; female flowers, neuter flowers, and seeds, × 10, S.F.n. 27842. The red tepals shown in black.

belong to *F. glandulifera*, and it lacked marginal teeth (Singapore Field n. 33000). There is variability among these plants which needs investigation because there may be, as in *F. carica*, races with deeply lobed, shallowly lobed, and even entire leaves. It is to be hoped that such common plants as *F. chartacea*, *F. fulva*, *F. grossularioides* and *F. hirta* will receive attention in southeast Asia.

Now, if the lobing be disregarded, this form of megaphyll with few effective pairs of lateral veins is clearly a reduction and modification from the obovate megaphyll such as occurs in the groups *Pharmacosycea*, *Pseudopalma*, *Adenosperma*, *Sycidium* and *Sycocarpus* (Corner 1967, 1969*b*). It is derived through limitation of apical growth and lamina development, compensated by the basipetal expansion to give the broadly cordate base with more numerous, basipetally developed, pairs of basal veins. But the pinnate and palmate lobing, along with the marginal toothing, as relics of the pinnate construction, show in subsect. *Eriosycea* a more primitive state than that of these other groups and one that approaches the primitive pinnate and pinnately lobed megaphyll of *Artocarpus*. Thus, subsect. *Eriosycea* illustrates the way in which the primitive form of the fig-leaf can be modified during the pachycaul stage before simplifying into the small leaves of the advanced leptocaul. These small leaves, often with some coarse teeth, lobes or angles (figures 9, 10), recall the leptocaul leaves in other groups of *Ficus* and, indeed, of Moraceae for which there may be no pachycaul survivors to indicate their origin, e.g. *F. celebensis*, *F. goniophylla*, *F. heteropleura*, *F. obscura*, *F. sinuata* and *F. tinctoria* in various groups of sect. *Sycidium*, as

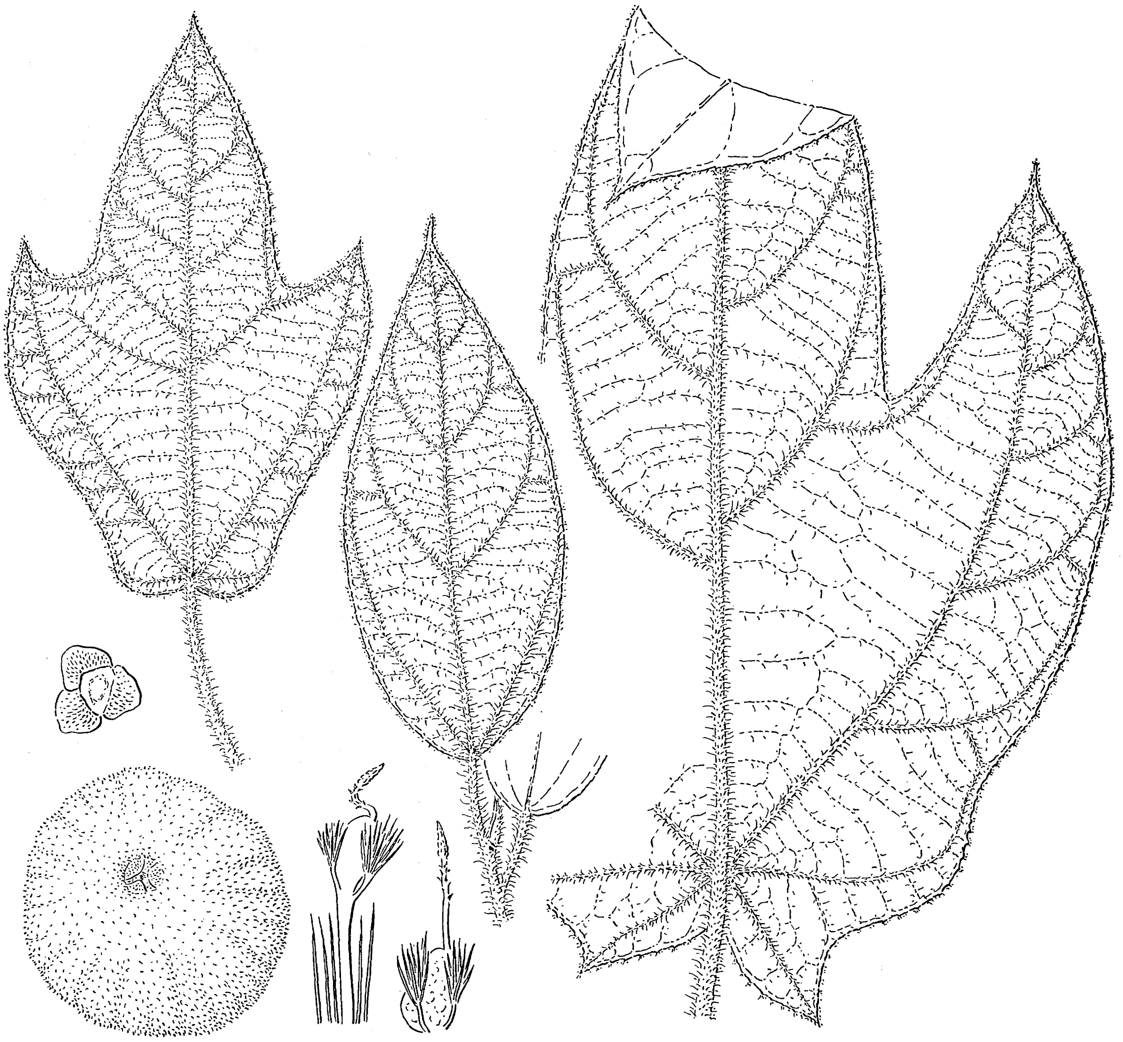

FIGURE 6. *F. brunneo-aurata*, palmately lobed sapling leaf (Corner s.n., 1959) and simple adult leaves (S.F.n. 25125), × $\frac{1}{2}$; fig with basal bracts, × 3, and female flowers, × 10, S.F.n. 25125.

well as *Antiaropis* and *Sparattosyce* (Corner 1969*a*) and *Streblus* (Corner 1962). Many parallels could be cited from the great assemblage of Tiliales, Malvales and Euphorbiales, such as *Hibiscus*, *Sterculia*, *Scaphium*, *Tarrietia* and *Jatropha*, for the leaves of these orders are also based on the palmate or palmatifid form. Most of their genera have become leptocaul with simple elliptic leaves, as in the euphorbiaceous *Aporosa* which is frequently mistaken for *Ficus*, and such simple leaves may give no evidence by themselves how they have been derived from the palmate. Thus it happens, erroneously in my opinion, that a species of *Platanus* with lanceolate leaf can be regarded as primitive (Baas 1969). To find out the course of evolution the big genera must be studied, which is what morphologists dislike because of the magnitude of the undertaking and the difficulties in identification. The big genera, variously delayed in their evolution, retain the intermediates between the rare pachycaul ancestry and the host of leptocaul derivatives.

The commonly quoted law of Dollo, that characters lost are not regained, may be applicable in these cases for the leptocaul do not seem naturally to have reverted to the pachycaul or the microphyll to the megaphyll, but the developmental properties of stem and leaf seem rather to be subjugated and limited in the leptocaul, as by hormonal control, than lost; and it may be possible experimentally through tissue-culture to restore *F. chartacea*, for instance, to the pachycaul form with the large, many-veined, obovate, but pinnately lobed, lamina. Some of the possibilities are effected in a small way by insect-galls, one of the most frequent being the restoration of hairs in glabrous species. Yet, among the more leptocaul species, there is a tendency of the lamina to vary into races with lanceolate leaf in which intercalary growth is reduced while apical growth is restored to the maximum of 12–20 effective pairs of lateral veins (figures 7, 17). While Dollo's law represents the contracting spiral of specific evolution, physiology should be able to restore at any point a tangent.

Accounts of *Ficus* are still apt to repeat the Englerian description of the leaves as convolute in bud. This is the shape of simplified leaves with basipetal extension of the intercostal areas towards the midrib; such leaves push their margins outward from the midrib and they circle round within the embracing stipules. The leaves with transverse intercostals, such as in sect. *Ficus* and particularly subsect. *Eriosycea*, are plicate in bud, as those of *Artocarpus*. The reason for this has not been investigated, but the convolute venation implies advance in leaf-development. Thus, the form and venation of the leaf of *F. elastica* resembles superficially that of *Musa*.

Ser. *Auratae*

This is the more readily distinguished and geographically circumscribed series of subsect. *Eriosycea*. The 11 species are Bornean but *F. aurata* ranges into Sumatra, Malaya and Palawan (table 1). The series has the primitive equipment of copious internal bristles and setose flower pedicels (Corner 1970), but the main character is the more or less complete conversion of the tepals of the gall and female flowers into colourless, stalked clusters of setae; in subser. *Monandreae* this feature extends also to the male tepals. The effect is a fig so intensely bristly that it is not clear how animals may eat it or insects enter it. Then the hairs on the stems and leaves turn golden to ferruginous yellow on drying, as happens generally with the leaf tissue, and this colour is a useful herbarium guide.

In ser. *Eriosyceae* the tepals in all the flowers are red, fleshy and glabrous or merely ciliolate round the apex. This is the usual state in sect. *Ficus*. It is at once obvious on cutting open the fig, living or dried, and it is the only certain way to distinguish *F. aurata* (colourless setose tepals) from *F. fulva* and *F. hirta* with which it has often been confused. There are, nevertheless, several steps in this transformation of the tepals in ser. *Auratae*, and herein lies the importance of the new species *F. diamantiphylla*. Thus:

Subser. *Auratae*; male tepals not setose, sometimes ciliolate; stamens 2; sapling leaves often palmately lobed.

(*a*) Male and neuter tepals red.

(i) Tepals of female flowers red, fleshy, setose distally (gall tepals?); *F. diamantiphylla*.

(ii) Tepals of gall and female flowers colourless, setose, not fleshy; *F. bruneiensis*, *F. brunneo-aurata*, *F. endospermifolia* (figures 4 to 6).

(*b*) Male and neuter tepals pale pink or white; gall and female tepals colourless, setose; *F. aurata* (figure 7), *F. aureocordata*.

Subser. *Monandreae*; male tepals colourless, setose as the gall and female tepals; stamen 1; sapling leaves not palmately lobed; *F. androchaete*, *F. eumorpha* (?), *F. macilenta*, *F. paramorpha*, *F. setiflora* (figures 8 to 13).

TABLE 1. SPECIES OF SER. *AURATAE*

	twig (mm)	leaf lat. veins pairs	sapling leaf	fig (dried) (mm)	habitat	distribution
subser. *Auratae*						
F. diamantiphylla	6–10	7–8	lobed	20–25 × 13–14	lowland	Brunei, Sarawak
F. bruneiensis	6–12	5–6	?	24–30 × 20–26	lowland	Brunei, Sarawak
F. endospermifolia	4–7	4–5	lobed	18–25 × 15–20	mountain	Kinabalu
F. brunneo-aurata	3–6 (–10)	4–5	lobed	11–16	lowland mountain	Borneo generally
F. aureocordata	5–6	5–6	?	17	mountain	central Borneo
F. aurata	2.5–5	5–7 (–20)	not lobed	10–12	lowland	Malaya, Sumatra, Borneo, Riouw, Bangka
v. *palawanensis*	?	4–6	lobed	14–18	lowland	Palawan, Sabah?
subser. *Monandreae*						
F. androchaete	3–4	4–5	not lobed	12–15	lowland	north Borneo
F. eumorpha	4–5	5–8	not lobed	16–17 × 14–15	mountain	north Borneo
F. paramorpha	2–3	5–6	not lobed	9–10	mountain	Kinabalu
F. macilenta	2–3	4–8	not lobed	8–9	mountain	north Borneo
F. setiflora	1.5–2	5–7	not lobed	7–9	mountain	north Borneo

If this information is combined with that given in table 1, it can be seen that:

(1) The least modified state of the perianth and of the male flowers goes with the pachycaul character in the diandrous subser. *Auratae*.

(2) The most modified state of the perianth and of the male flower goes with the leptocaul character in subser. *Monandreae*.

(3) The pachycaul *F. diamantiphylla* has the perianth of ser. *Eriosyceae* except for the marginal setae; it is the link between the two series, but it is to be placed in ser. *Auratae* because of the indumentum (long golden hairs, double indumentum, velutinate veins).

(4) The one truly leptocaul species of subser. *Auratae*, namely *F. aurata*, has the most advanced male perianth, approaching that of subser. *Monandreae*, and it is the one species ranging outside Borneo.

(5) The more pachycaul species, with less advanced perianth, are strictly limited geographically in the manner of primitive pachycaul survivors, namely *F. bruneiensis*, *F. diamantiphylla*, *F. endospermifolia*.

(6) The most leptocaul species of the more advanced subser. *Monandreae* are mountain species of restricted distribution, namely *F. macilenta*, *F. paramorpha* and *F. setiflora* (unfortunately, male plants of *F. eumorpha* are not known).

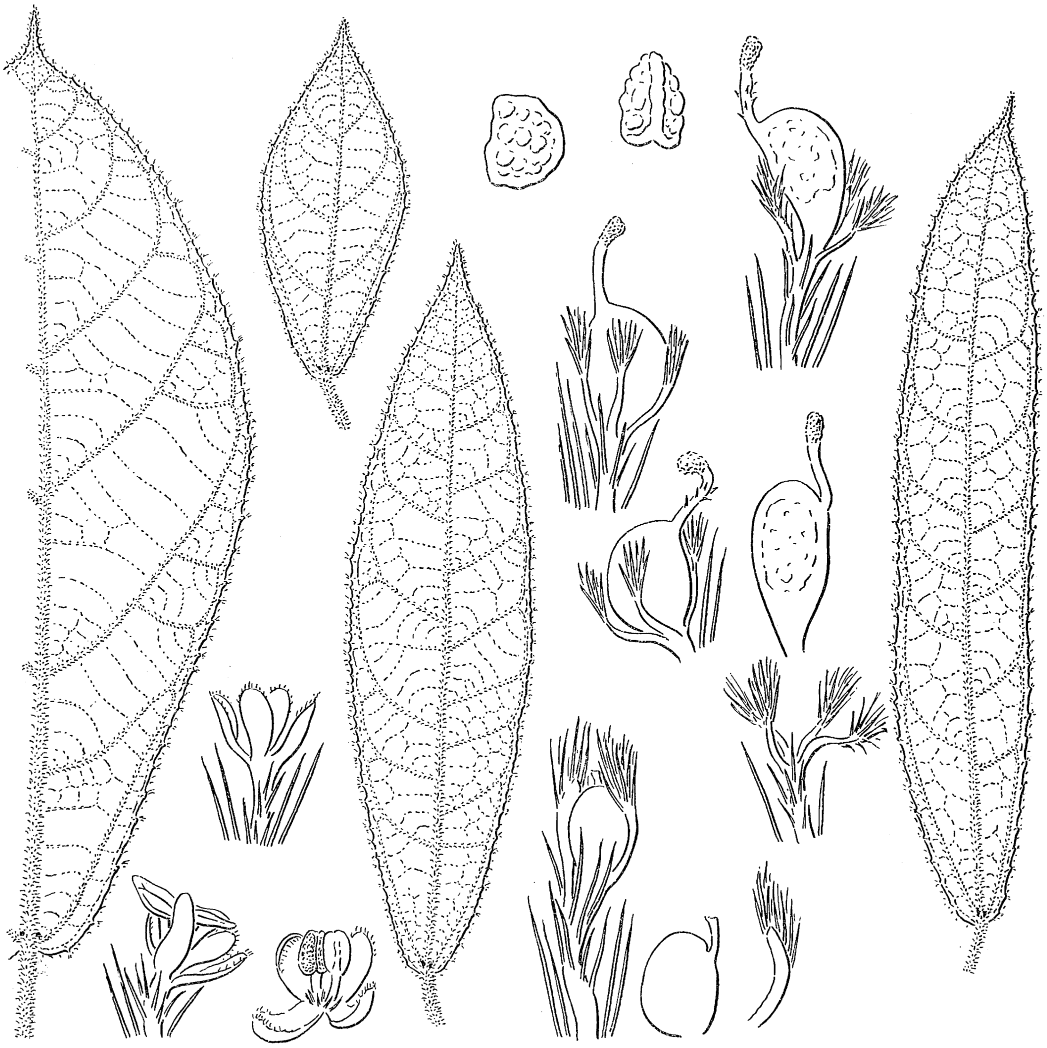

FIGURE 7. *F. aurata*, leaves of various Malayan collections to show the tendency from the usual obovate form to the oblong and lanceolate, × ½; flowers and seeds from living plants in Singapore, × 10.

F. aurata. This is a common shrub or small tree of secondary growth in Malaya, Sumatra, the Riouw archipelago, Bangka and Borneo; it may be represented by a variety in Palawan. It has not been found in the well collected floras of Java, Thailand and the Philippines. In Malaya it has not been found north of Perak and Trengganu. There is a collection from Indo-china (Ch. d'Alleizette s.n., Nha Bang, Annam, June 1909), but the species was never encountered by the numerous indefatigable French collectors of *Ficus* in Indo-China and I must assume that it is a mistaken locality, just as with the record from Chittagong (King's collector s.n., 1886). This distribution coincides with that of *F. deltoidea* var. *angustifolia* (Corner 1969*a*, figure 1), except that *F. aurata* does not enter lower Thailand. Indeed, the whole distribution of ser. *Auratae* agrees closely with that of *F. deltoidea*, apart from the absence from Java; it shows the pachycaul concentration in Borneo where var. *motleyana* represents the beginning of the *F. deltoidea* complex. I regard *F. aurata* as the adaptable species of late origin that has spread along with *F. deltoidea* var. *angustifolia*, unlike the restricted and primitive pachycaul *F. diamantiphylla* and the rather less primitive *F. bruneiensis*, *F. endospermifolia* and *F. aureocordata*. These species pose the usual problem why the pachycaul should be so restricted. *F. endospermifolia* is a fairly common tree at mid-altitude on the southern slopes of Mt Kinabalu, but it has not been found elsewhere. It appears as a montane derivative of the lowland *F. bruneiensis* which occurs rarely as a riverside tree in the interior forest of Brunei and the neighbouring division of Sarawak. *F. aureocordata* is known from a single collection from central Borneo (Bukit Raja, 1250 m; Corner 1960*a*). A collection of immature material (S. 17688) suggests yet another undescribed

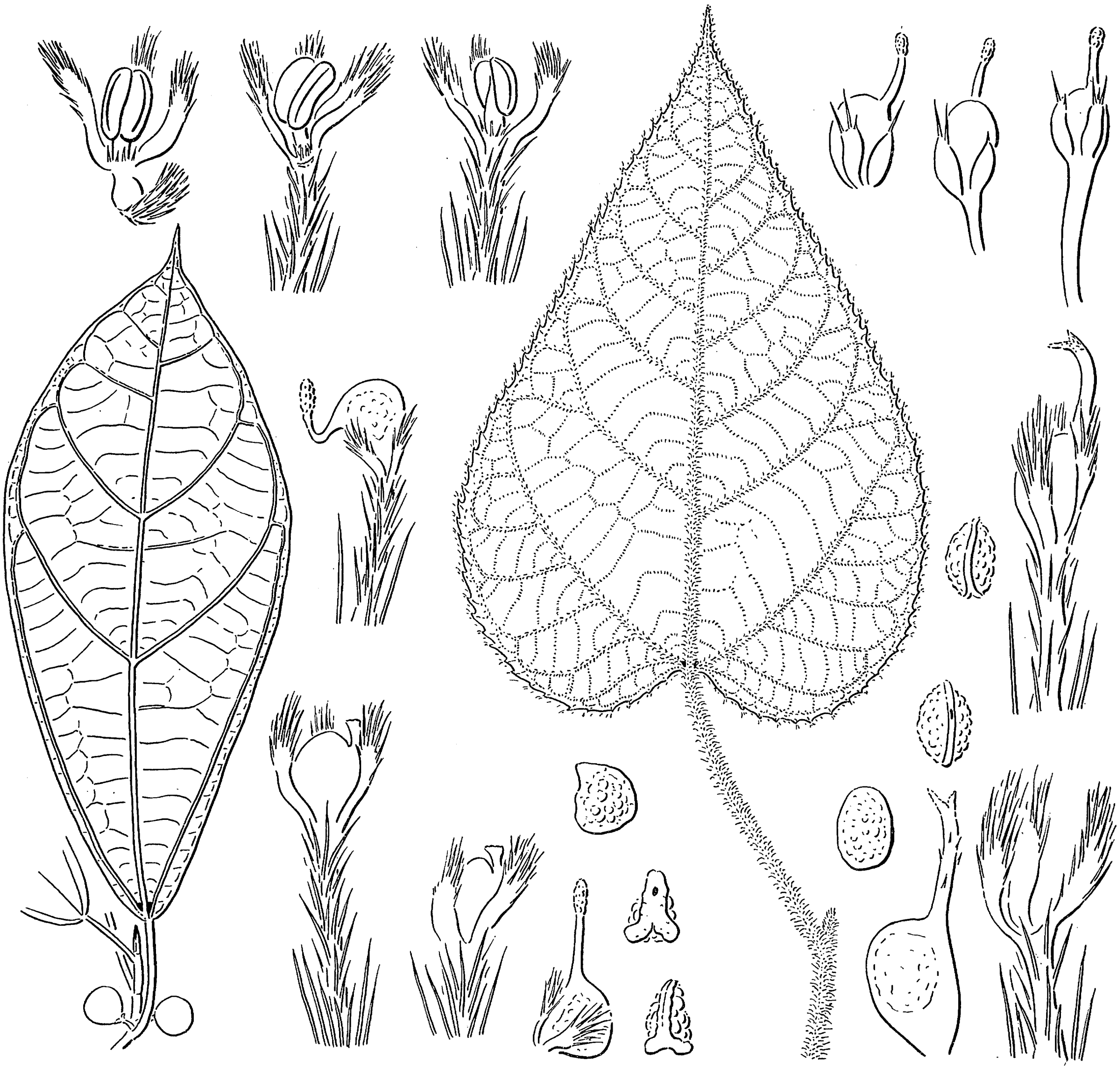

FIGURE 8. *F. androchaete* (left), leaf, × ½, Brunei 5320; male and gall flowers (Brunei 5320), female flowers and seeds (S. 22966), × 10. *F. eumorpha* (right), leaf, × ½; female flowers and seeds, × 10, S.F.n. 27566; upper right, female flowers of var. *subglabra*, × 10, Endert 4416.

ally as a tree of submontane forest in Sarawak. The alliance of all these species is very close and, conceivably, intermediates still exist. Actually the species that comes nearest to *F. aurata* is *F. brunneo-aurata*. It is widely distributed in lowland secondary forest in Borneo, perhaps also in the mountains for there is a record (San 44337) from Trus Madi at 2000 m in Sabah, and it may give the clue to the ecological emancipation from the pachycaul forest trees.

Subser. *Monandreae*. This subseries appears advanced in every way except for the tendency to retain the peduncle of the fig. The leptocaul habit, the small leaves which are never palmately lobed, the reduced intercostal veining, the cuneate leaf-base, the setose modification of the male perianth, the reduction to the single stamen (as in sect. *Sycidium*), and the tendency to reduce the indumentum are advances that seem, in this case, to have gone with specialization to high mountain habitats. *F. androchaete* appears as the lowland forest representative of the ancestor of the subseries, to be related perhaps with the pedunculate ancestor of *F. aurata* and *F. brunneo-aurata*. As shown in table 1, the subseries is limited to the northern part of Borneo.

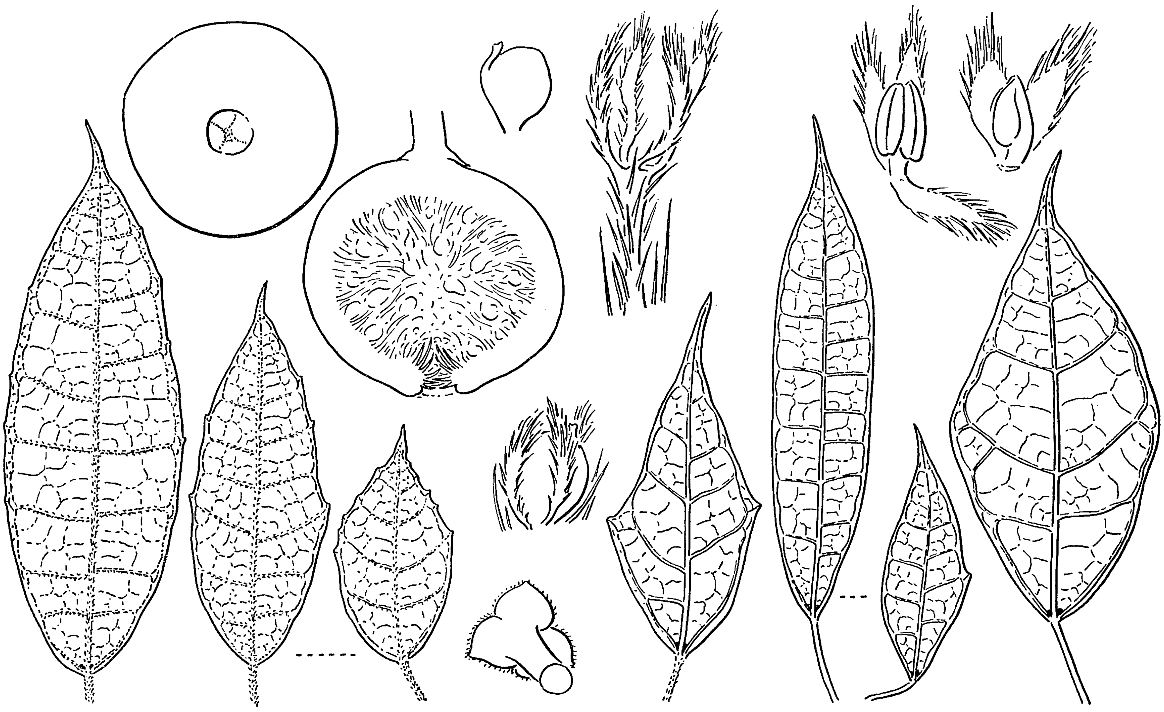

FIGURE 9. *F. macilenta*, leaves of var. *macilenta* (left, Beccari 1696 with two leaves of Ridley 11665) and of var. *gibbseae* (right, Clemens 51746 with two narrow leaves of S.F.n. 28018), × ½; fig of var. *gibbseae*, × 3, with male and gall flowers, × 10, S.F.n. 28018.

Pedunculate fig. In subser. *Auratae* the figs are sessile except for *F. aurata* var. *pedunculata* which is limited to central Malaya (Perak, Trengganu, Selangor). In subser. *Monandreae* the fig is more or less pedunculate in *F. androchaete*, *F. macilenta* and *F. setiflora*. It seems that the character has been variously lost, as in ser. *Eriosyceae*, and the ancestral pachycaul state had a pedunculate fig and red tepals; it must have resembled *F. fulva* (figure 16).

Vicariism. Four more or less primitive, pachycaul species occur in central and north Borneo without, so far as known, any overlap in their distribution. They are *F. aureocordata*, *F. bruneiensis*, *F. diamantiphylla* and *F. endospermifolia*. If they are assumed to have a vicarious origin from a widespread ancestor, then there is no evidence of it unless *F. brunneo-aurata* is its descendent. This species, however, is the more versatile adaptation to secondary forest; it lacks the primitive red tepals of *F. diamantiphylla* and, in its more leptocaul state, it has smaller leaves, figs and basal bracts than the other three species. In all these features the more widespread *F. aurata* is even less able to qualify as this ancestor and, in its particular case, there is *F. aureocordata* as the pachycaul predecessor in central Borneo. Now *F. aurata* is variable and the question rises whether its varieties show vicariism. Three of the five varieties are restricted; var. *brevipilosa* is in north Borneo, var. *palawanensis* in Palawan and perhaps north Borneo, and var. *pedunculata* is Malayan. With the exception of Palawan, var. *aurata* occurs throughout the areas of these varieties and there is no evidence that this successful one is displacing the others or being displaced by them. Subser. *Monandreae* offers no better evidence. Four of the mountain species occur on Mt Kinabalu where I have seen three of them growing in the forest round the Mesilau River at 1500–2000 m alt. They are not common. As bushes or small trees on rocks and declivities, they are

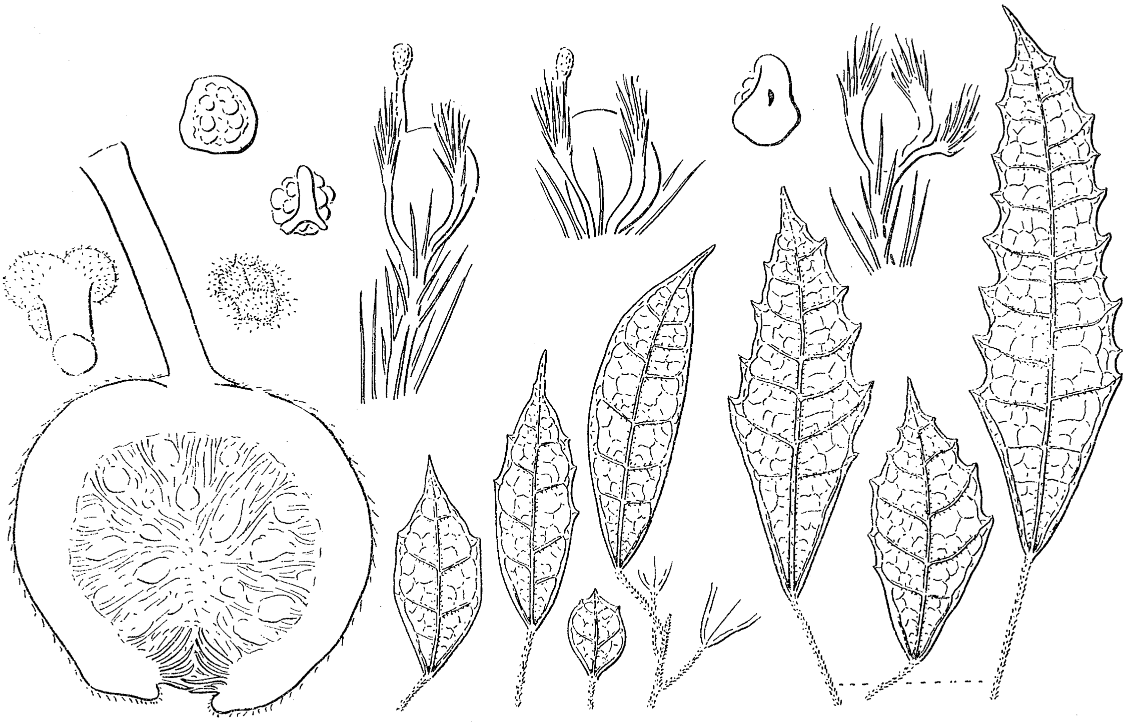

FIGURE 10. *F. macilenta* var. *ilicifolia*, leaves, × ½; fig and basal bracts, × 3; female flowers and seeds, × 10; S.F.n. 26952 with three leaves (right) of RSNB 2648.

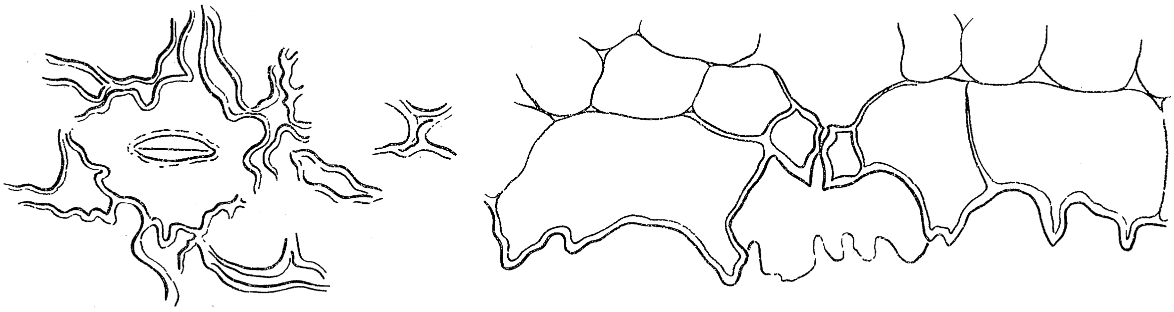

FIGURE 11. *F. macilenta* var. *ilicifolia*, stomata, × 800.

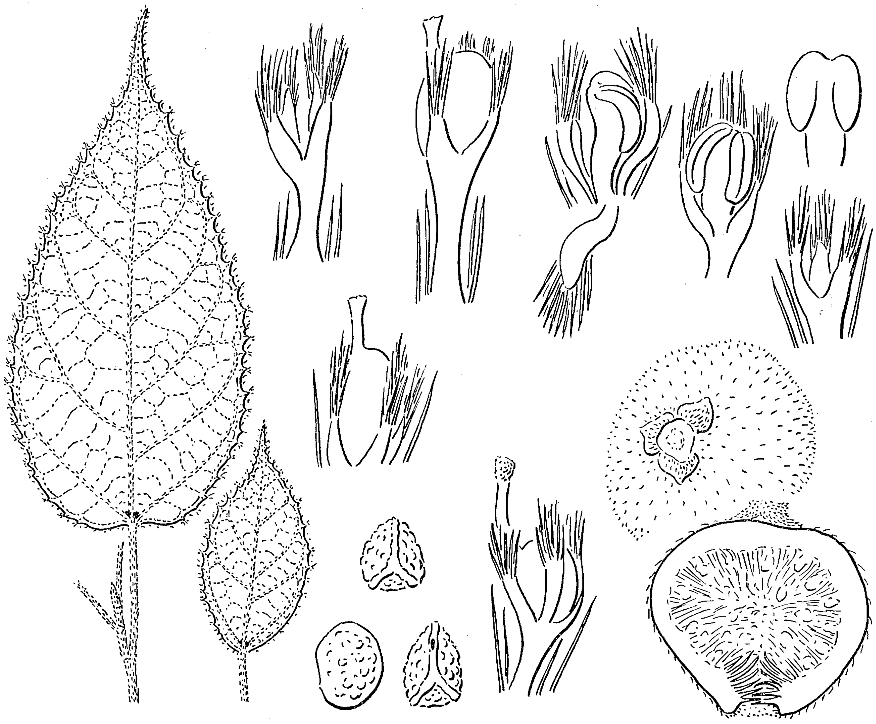

FIGURE 12. *F. setiflora*, leaves, ×½; figs, ×3; male and gall flowers, ×10, S.F.n. 27513; female flowers and seed, ×10, Carr. s.n. 1933.

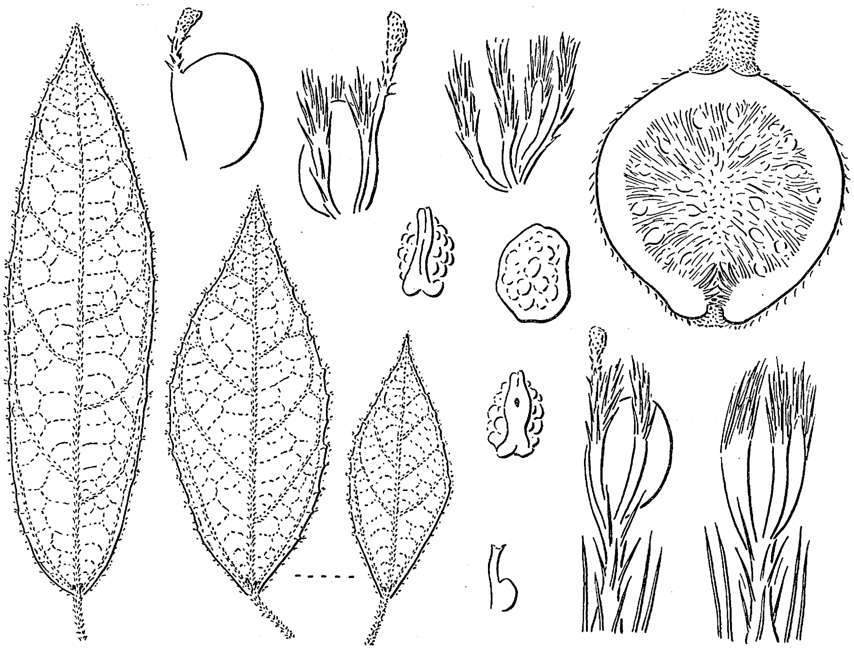

FIGURE 13. *F. setiflora* var. *adelpha*, leaves, ×½, Clemens 28433 with two leaves of S.F.n. 27876; fig, ×3, female flowers and seeds, ×10, S.F.n. 27876.

spaced by tracts of tall, dense forest; they are not like the similar bushes of *Rhododendron* or *Vaccinium* which may occupy considerable tracts of the undergrowth. *F. setiflora* may favour the tops of fallen rocks, *F. eumorpha* the flanks, and *F. macilenta* the screes, but there are plenty of such places where they do not occur. Their distribution is not vicarious but fortuitous within this extremely complicated terrain. Though once considered to be endemic on Kinabalu, both *F. eumorpha* and *F. setiflora* have been found on the mountains of Sarawak and West Koetai. *F. macilenta*, first found on Gunong Matang near Kuching, has been found on G. Mulu and in two varieties on Kinabalu. Whether these mountains offer any vicarious distribution remains to be explored.

F. diamantiphylla sp. nov. (figure 14) (check-list no. 199A)

Arbor ad 7 m alta, foliis spiraliter dispositis. Indumentum duplex; pilis 2–5 mm longis, rigidis, aureis v. ferrugineis ad ramulos stipulas petiolos costas et syconia strigoso-tomentosis; pilis minutis 0.1–0.2 mm longis, hyalinis, ut substratum velutinum sub pilis longis, venulis modo plus minus velutinosis. Ramuli 6–10 mm crassi. Stipulae 15–30 mm longae, subpersistentes. Lamina 40–50 × 20–26 cm, elliptico-obovata plus minus diamantiformis, breviter acuminata, ad basim anguste cordatum attenuata, denticulata membranacea subscabrida, sicco fuscoviridis; costis lateralibus utrinsecus 7–8, sparsim longipilosis, prominentibus; intercostis 6–12, prominentibus, villosulis v. velutinosis; venulis reticulatis subglabris; areolis planis glabris; costis basalibus ultrinsecus 4–5, majoribus elongatis; petiolo 3–10 cm longo; glandulis basalibus 2, subnodalibus? Receptacula axillaria sessilia, dense strigosa, maturitate rubra; bracteis basalibus, 3, 3–5 mm longis, ovatis, breviter appresse brunneo-pilosis; corpore 20–25 × 13–14 mm (sicco), ellipsoideo, bracteis lateralibus strigosis paucis 1.5–2.5 mm longis ostiolum versus instructo; setis internis ad 1.5 mm longis, copiosis albis subsericeis; cellulis scleroticis in pariete nullis. Flores masculi et cecidiophori? Flores neutri sessiles ostiolares; tepalis rubris, ad apicem ciliato-pilosis. Flores feminei sessiles var. pedicellis albis pilosis ad 1.5 mm longis praediti; tepalis 3–4 intense rubris succosis, lanceolatis v. spathulatis, ad apices setis ad 0.8 mm longis dense strigosis; ovario sessili v. breviter stipitato; stylo piloso, stigmate breviter bifido. Semina 1.2–1.4 mm longa, tuberculata, obtuse carinata. Cystolitha nulla. In silvis Sarawak; typus, M. J. Hotta 12879, Seria district, Teraja, 300–400 m alt., 21 Dec. 1963 (CGE Kyoto); S. 22791, Sungei Langsat, Ulu Tutoh, 4th Division, leg. J. A. R. Anderson, 9 Feb. 1966.

As a pachycaul species, this offers a primitive combination of characters in the large leaf, the subpersistent stipules, the long hairs, the subapical lateral bracts, the soft internal bristles and the red fleshy tepals. The last two characters ally it with subser. *Trichosyceae*, but the golden hairs, double indumentum, leaf shape, and setose tepals place it with subser. *Auratae*.

Ser. ***Eriosyceae***

This series of 19 species is more varied and more widespread than ser. *Auratae*. Four species are Indo-Chinese, namely *F. esquiroliana*, *F. langkokensis*, *F. simplicissima* and *F. tuphapensis*. The remainder fall within the compass of the Flora Malesiana and I shall treat them here only in so far as concerns the origin of subsect. *Eriosycea*. The problem is outlined in table 2. The three main subseries have the following unexpected differences:

Subser. *Dehiscentes*; gall-figs dehiscent, ripening green or yellowish (figure 15); seed-figs indehiscent, ripening yellow to red; leaves entire, not palmately lobed (or perhaps in the sapling), not white tomentose beneath.

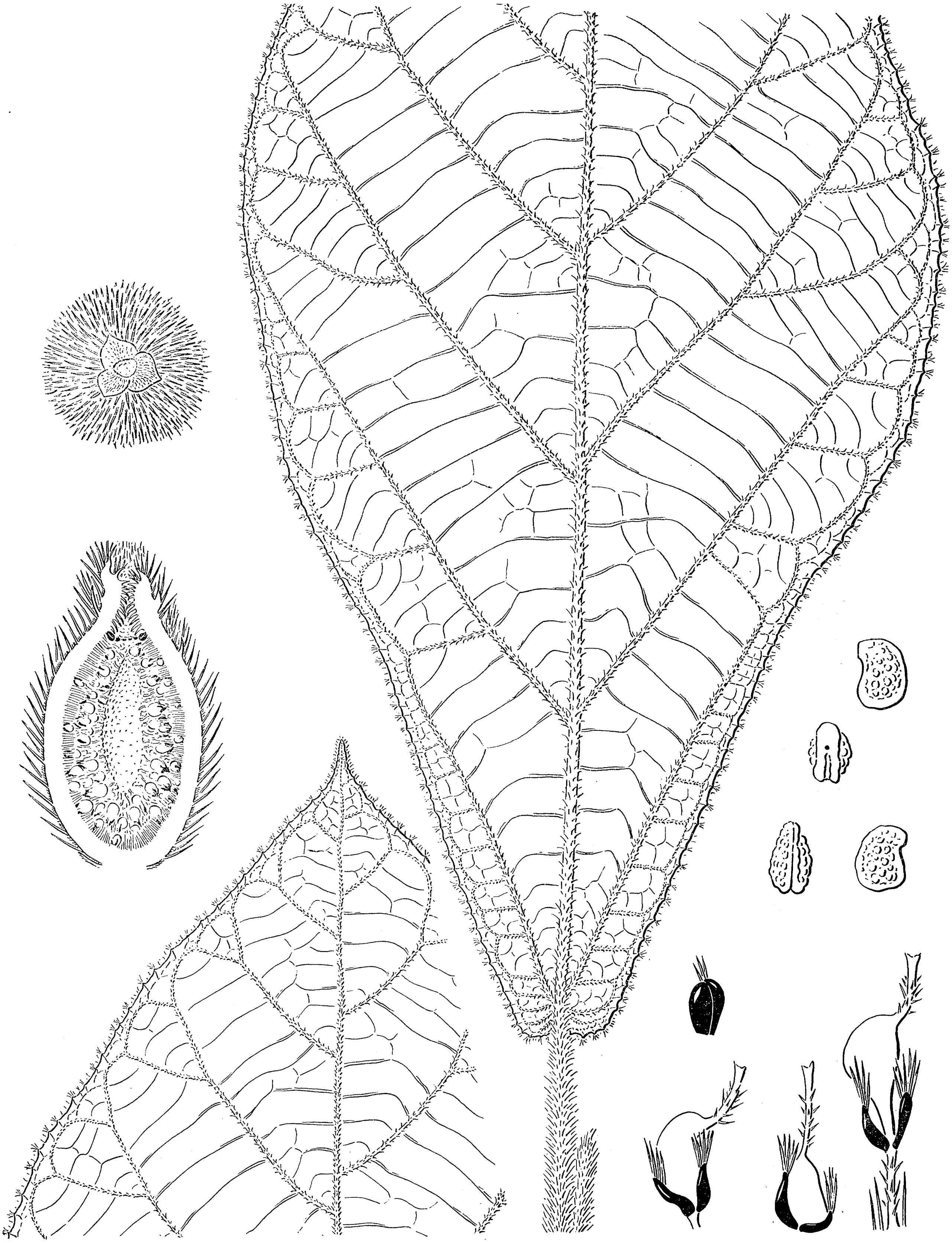

FIGURE 14. *F. diamantiphylla*, leaf, × ½; figs, × 2; female flowers and seed, × 10; M. Hotta 12879. The red tepals shown in black.

Subser. *Trichosyceae*; gall- and seed-figs indehiscent, ripening yellow to red; leaves dentate, often palmately lobed (at least in the sapling), not white tomentose beneath.

Subser. *Eriosyceae*; as subser. *Trichosyceae* but the leaves white tomentose beneath with undulate hairs.

Subser. *Cuneifolieae*; probably an artificial group of leptocaul derivatives (p. 373).

The distribution of subser. *Dehiscentes* agrees with that of ser. *Auratae* in having a pachycaul centre, but it is shifted from Borneo to the triangle Borneo–Philippines–Celebes. This is the range of the pachycaul *F. ruficaulis* (figure 15) and in this range it is accompanied by *F. glandulifera* while *F. lamponga* (figure 15) seems to be absent from the Philippines. They are trees of primary and secondary forest. There is no evidence that they are vicarious. *F. lamponga* and *F. glandulifera* often grow in the same patches of forest throughout Malaya. The first extends to Assam, the second to New Guinea. This is the widest geographical range for any group of subsect. *Eriosycea* and suggests an early derivation with the most primitive status. Two structural features support the conclusion. First, the leaves are more advanced than those of subser.

TABLE 2. DISTRIBUTION OF THE SPECIES OF SER. *ERIOSYCEAE*

	Ass	Bur	Ch	I-Ch	Th	Mal	Sum	Jav	Bor	PI	Cel	Mol	NG
subser. *Eriosyceae*													
F. padana	.	.	.	.	.	.	—	—	.	.	.	.	.
F. grossularioides	.	.	.	.	—	—	—	—	—	.	.	.	.
F. tricolor	.	.	.	.	.	—	—	—	—	.	.	.	.
F. esquiroliana	.	.	—	—	—	.	.	.	.	.	.	.	.
	0	0	1	1	2	2	3	3	2	0	0	0	0
subser. *Trichosyceae*													
F. hirta	—	—	—	—	—	—	—	.	.	.	.	.	.
var. *roxburghii*	—	—	—	—	—	.	.	.	.	.	.	.	.
var. *squamosa*	.	.	.	.	.	.	—	.	.	.	.	.	.
F. schefferiana	.	.	.	.	.	.	—	.	.	.	.	.	.
F. simplicissima	.	.	?	—	.	.	.	.	.	.	.	.	.
F. halmaherae	.	.	.	.	.	.	.	.	.	.	.	—	.
F. mollissima	.	.	.	.	.	—	.	.	.	.	.	.	.
F. fulva	.	.	.	.	—	—	—	—	—	.	—	—	.
F. subfulva	.	.	.	.	.	.	.	.	—	.	.	.	.
	1	1	1	2	2	3	3	1	2	0	1	2	0
subser. *Dehiscentes*													
F. ruficaulis	.	.	.	.	.	.	.	.	—	—	—	.	?
F. glandulifera	.	.	.	.	.	—	—	—	—	—	—	—	—
F. lamponga	—	—	.	—	—	—	—	.	—	.	—	.	.
	1	1	0	1	1	2	2	1	3	2	3	1	1
subser. *Cuneifolieae*													
F. chartacea	.	—	—	—	—	—	—	.	—	.	.	.	.
F. litseifolia	.	.	.	.	.	—	—	.	.	.	.	.	.
F. oreophila	.	.	.	.	.	—	.	.	.	.	.	.	.
F. tuphapensis	.	.	—	—	—	.	.	.	.	.	.	.	.
F. langkokensis	—	.	—	—	.	.	.	.	.	.	.	.	.
	1	1	3	3	2	3	2	0	1	0	0	0	0
ser. *Eriosyceae* total	3	3	5	7	7	10	10	5	8	2	4	3	1
ser. *Auratae* total	0	0	0	0	0	1	1	0	11	1	0	0	0
subsect. *Eriosyceae* total	3	3	5	7	7	11	11	5	19	3	4	3	1
endemic				1		2	1		10			1	

Ass, Assam; Bor, Borneo; Bur, Burma; Cel, Celebes; Ch, China; I-Ch, Indo-China; Jav, Java; Mal, Malaya; Mol, Moluccas; NG, New Guinea; PI, Philippines; Sum, Sumatra; Th, Thailand.

Eriosyceae and *Trichosyceae*, and this indicates an earlier origin to allow sufficient time for the advance. Secondly, the dehiscent gall-fig may be a primitive character not only in subgen. *Ficus* but in the whole genus. The analogy is with the dehiscent, non-blastophagous syconium of *Sparattosyce*. Though subgen. *Ficus* is the advanced dioecious subgenus with less extensive distribution than subgenera *Urostigma* and *Pharmacosycea*, its ancestor must have persisted with primitive status in the lobed and dentate leaf, the male flower, and the syconium long after the other subgenera had evolved, dispersed and, in the main, lost the primitive features. Subser. *Dehiscentes* must relate with this ancestor and, remarkably, it agrees with the most advanced group of subsect. *Eriosycea*, namely ser. *Auratae*, in referring the scene of evolution to the past history of north Borneo. The striking difference between these two groups lies in their speciation.

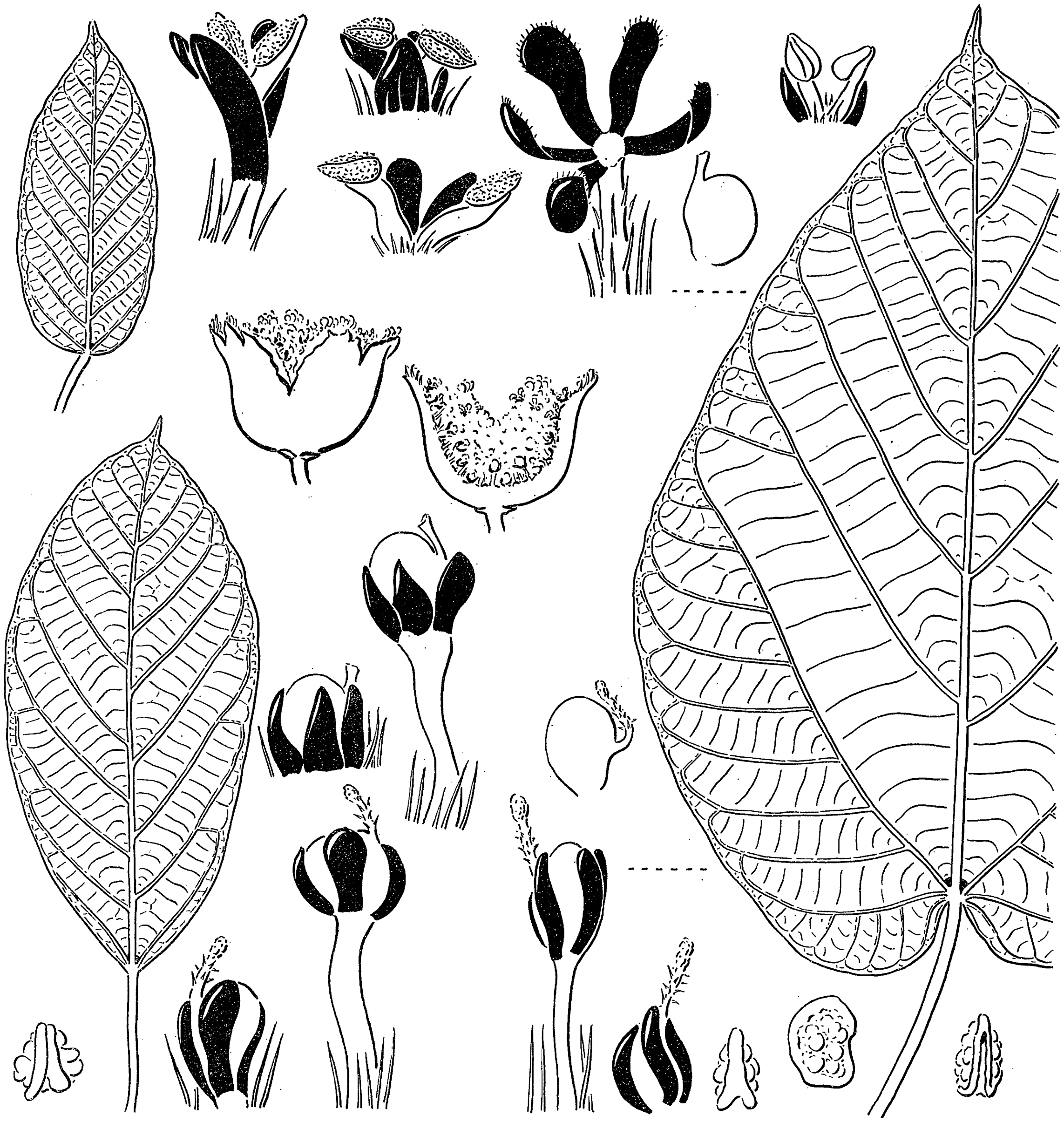

FIGURE 15. *F. lamponga* (left) with figs and *F. ruficaulis* (right); leaf, ×½; flowers and seeds, ×10. S.F.n. 29227, 34922, *F. lamponga*; Elmer 22271, PNH 6129, 18450, *F. ruficaulis*.

Subser. *Dehiscentes* has a much wider geographical range but survives with merely three species of small divergence; ser. *Auratae* is much more localized and has evolved extensively into, at least, 11 species.

Subser. *Eriosyceae* and *Trichosyceae* introduce a new problem for they have a double

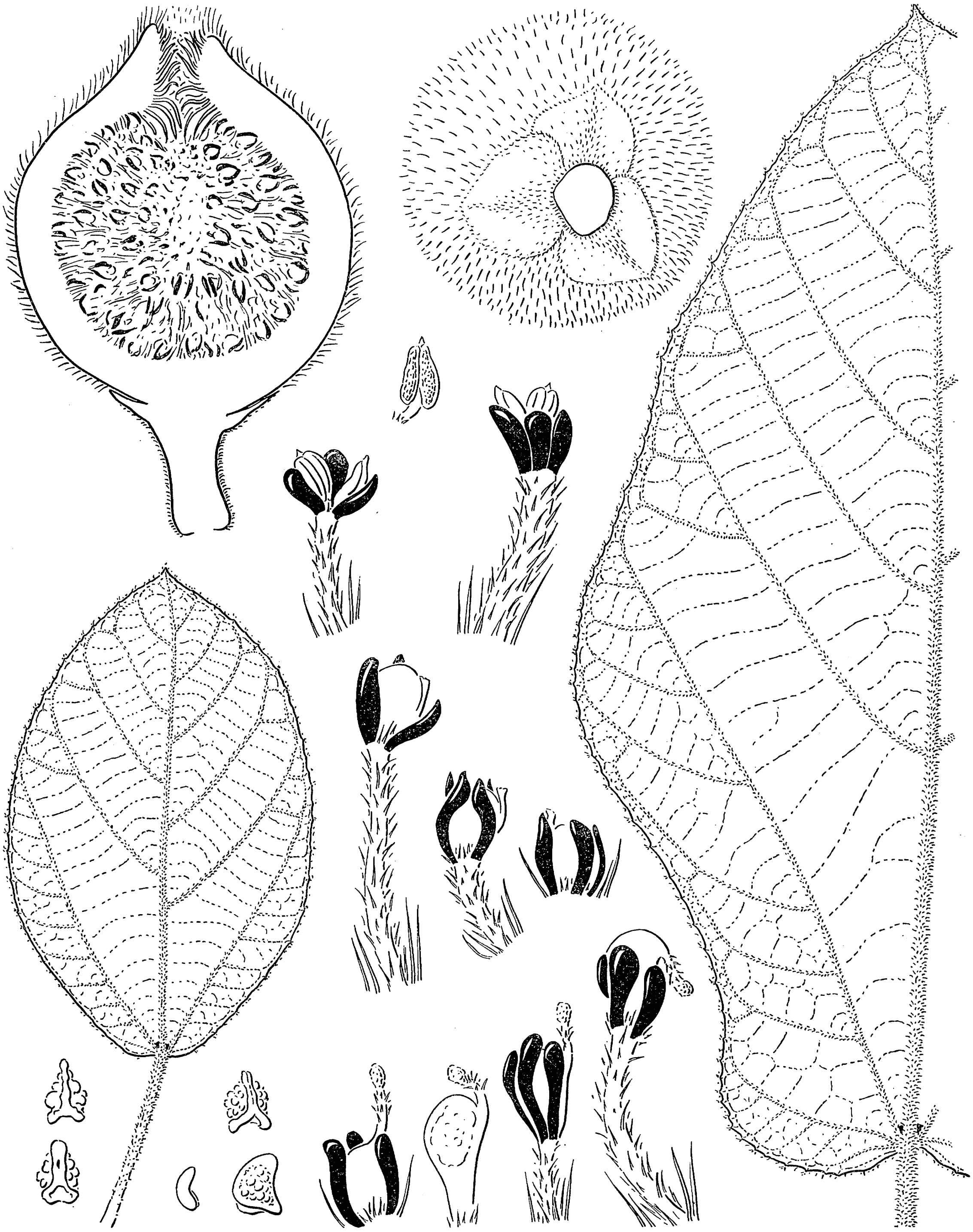

FIGURE 16. *F. fulva* from Malaya with sapling and adult leaves, ×½; figs, ×3; flowers and seed, ×10; Corner s.n., Negri Sembilan.

pachycaul base. One leg stands in the Indo-Chinese region, possibly in relation with the geological past of north Borneo, and the other is Malaysian. Subser. *Eriosyceae* has the pachycaul *F. esquiroliana* in Indo-China and the pachycaul *F. padana* in Sumatra and Java. Between and overlapping with *F. padana*, there are the two more derived species *F. grossularioides*, so common in lowland secondary forest, and the less abundant *F. tricolor* as a tree of mountain forest; it may be noted that what I have described from Malaya as *F. grossularioides* var. *robusta* (Corner 1960*a*) is no other than *F. tricolor*, as I have found on investigating fertile trees at Cameron Highlands in Malaya in 1966. The differences here are not merely north and south but lowland and mountain. If there were an ancestor that produced vicariously *F. esquiroliana* in the north and *F. padana* in the south, it may have extended along the mountains of the Malay Peninsula in the Tertiary period when they were less degraded, and have left *F. tricolor* in possession, but there is no evidence that it ever occurred in the lowlands which *F. grossularioides* has invaded so successfully. *F. tricolor* occurs in Sumatra and Java non-vicariously with *F. padana*. The solution is not simply one of vicariism.

Subser. *Trichosyceae* splits into two alliances. *F. hirta*, which is one of the commonest figs of subtropical southeast Asia, *F. schefferiana* and *F. simplicissima* are very closely related (Corner 1965, p. 45; Hill 1967); indeed, *F. schefferiana* and *F. simplicissima* may be only extremes of the very variable *F. hirta*. The trio shows, however, the north–south separation and *F. hirta*, itself, has two primitive and more or less pachycaul varieties comparable with and sometimes mistaken for *F. esquiroliana*. In Sino-Himalaya there is the stout var. *roxburghii* and in Sumatra there is var. *squamosa* which, alone, has stout lateral bracts on the fig (figure 2). The geographical history of *F. hirta* seems to repeat that of subser. *Eriosyceae* along the mountains of the Malay Peninsula but without having evolved a lowland representative.

The second alliance of subser. *Trichosyceae* consists of the Malaysian species *F. fulva*, *F. halmaherae*, *F. mollissima* and *F. subfulva*. Their distribution is given by that of *F. fulva* from Thailand to the Moluccas, excluding the Philippines, and it is not, therefore, vicarious: *F. fulva* is by far the commonest and most successful species. The most leptocaul species is *F. subfulva* of Borneo; the more pachycaul are *F. mollissima* (Malaya) and *F. halmaherae* (Corner 1960*a*, pp. 431–432). Both of these pachycaul species are, unfortunately, little known and the fragmentary material in herbaria is inadequate for illustration. There are two collections of *F. mollissima* (Kedah, Koh Mai Forest; Negri Sembilan, Triang). There is a single collection of *F. halmaherae* from Gunong Sembilan in Halmahera (Pleyte 369), but it bears the field-note '600 m alt., along path in forest, common'. The two species are close and have a peculiarity in the structure of the fig-wall which is composed of elongate, fibriform, sclerotic cells; in all other species of *Ficus* that I have studied in the world flora, these sclerotic cells are rounded. Though its leaf is denticulate, *F. halmaherae* resembles also *F. ruficaulis* and its gall-figs may be dehiscent. It is to be hoped that this remarkable tree, about the tallest in the subsection, may be rediscovered and adequately described before the Moluccan forests are annihilated. This Malayan alliance of subser. *Trichosyceae* provides another instance of two widely separate pachycaul species between which there stretches, in this case from east to west, the less pachycaul *F. fulva* as the common variable species of secondary forest, comparable with *F. grossularioides*. I conclude that somewhere on the mountains of Celebes or Borneo there exists the intermediate which will connect with *F. diamantiphylla* in ser. *Auratae*.

The fourth subser. *Cuneifolieae* consists of leptocaul species the derivation of which seems diverse. The common little shrub or tree of secondary forest in this case is *F. chartacea* (figure 17);

it is more or less glabrous and it seems to relate with *F. simplicissima* and *F. hirta*; the three need careful study where they overlap in Indo-China. Such a northern origin fits the sharp distribution of *F. chartacea* which forbids any facile assumption that species of *Ficus* are distributed at random. *F. chartacea* is common from south China to Singapore. It has never been collected in the Riouw or Lingga archipelagos or in Java. There are merely five records from central Sumatra (Asahan, Pajakumbuh, Tapianoeli) and five records from Borneo (Sandakan, Brunei, Miri, and central Borneo). *F. litseifolia* and *F. oreophila* (with rather large seed 1.5–2.5 mm wide, figure 18) of the mountains of Malaya and Sumatra are related with the Indo-Chinese *F. tuphapensis* (figure 19), but this species, though a much reduced leptocaul with frequently unistaminate male flowers, has cystoliths on the underside of the leaf. It agrees in this respect with the Indo-Chinese *F. langkokensis* (figure 20), which is even more divergent in having disperse male flowers and subechinulate seeds. All three features must be primitive for the evolution of subsect. *Eriosycea*. They suggest that *F. langkokensis*, *F. litseifolia*, *F. oreophila* and *F. tuphapensis* are the leptocaul relics of the extinct ancestry of the subsection and that this is to be read with that of ser. *Podosyceae* (Corner 1969*a*, p. 293). So far as I could determine from the hard and

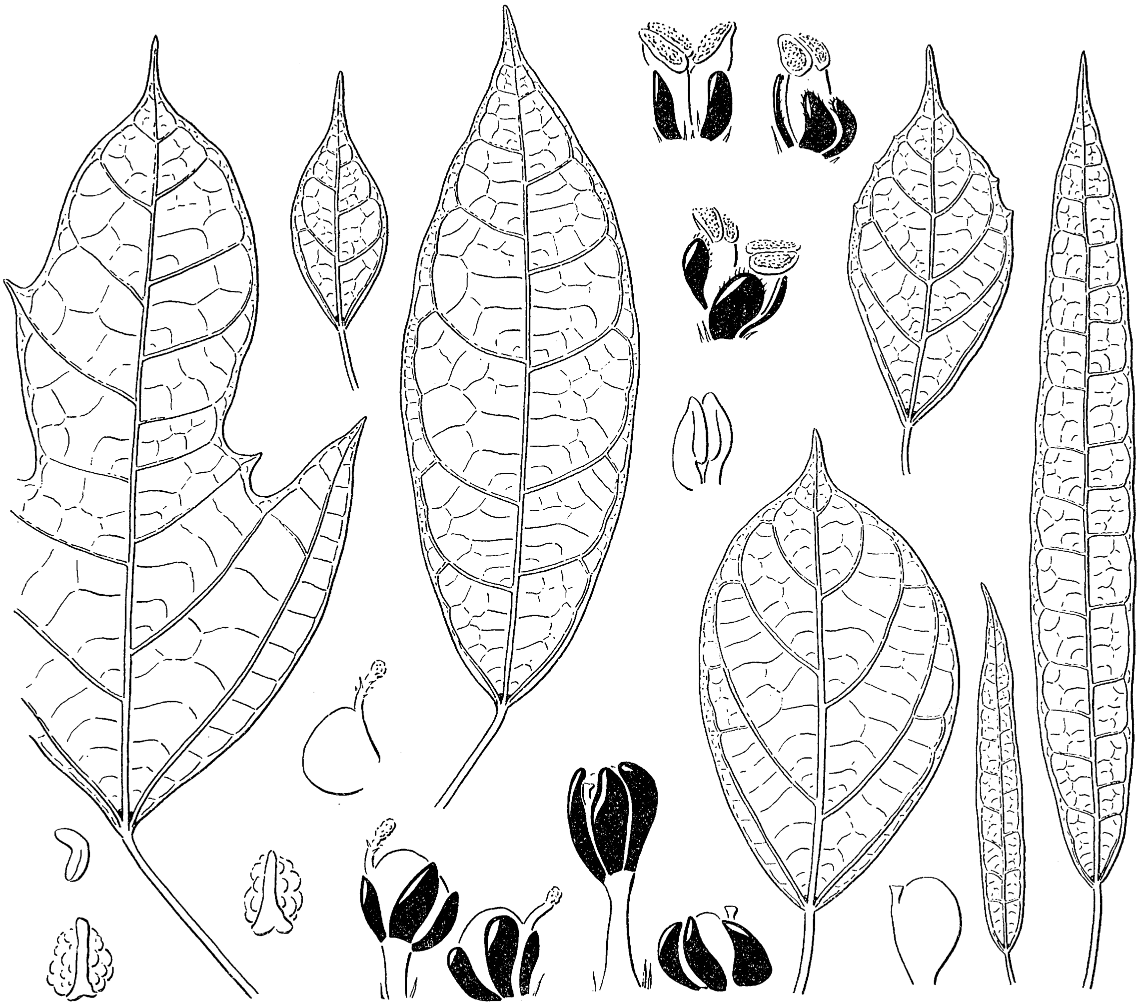

FIGURE 17. *F. chartacea* with lobed sapling leaf, three forms of adult leaf and two lanceolate leaves of var. *lanceolata*, × ½; flowers and seeds, × 10.

brittle, dried seeds of *F. langkokensis* the endocarp has a layer of radially elongate cells, typical of subsect. *Eriosycea*, though narrow, but the small excrescences of the endocarp are made of rounded sclerotic cells loosely clumped on the radial layer. Such details are important but are scarcely to be ascertained from dried material; for accurate sections, immature material with softer seeds, preserved in alcohol, is required.

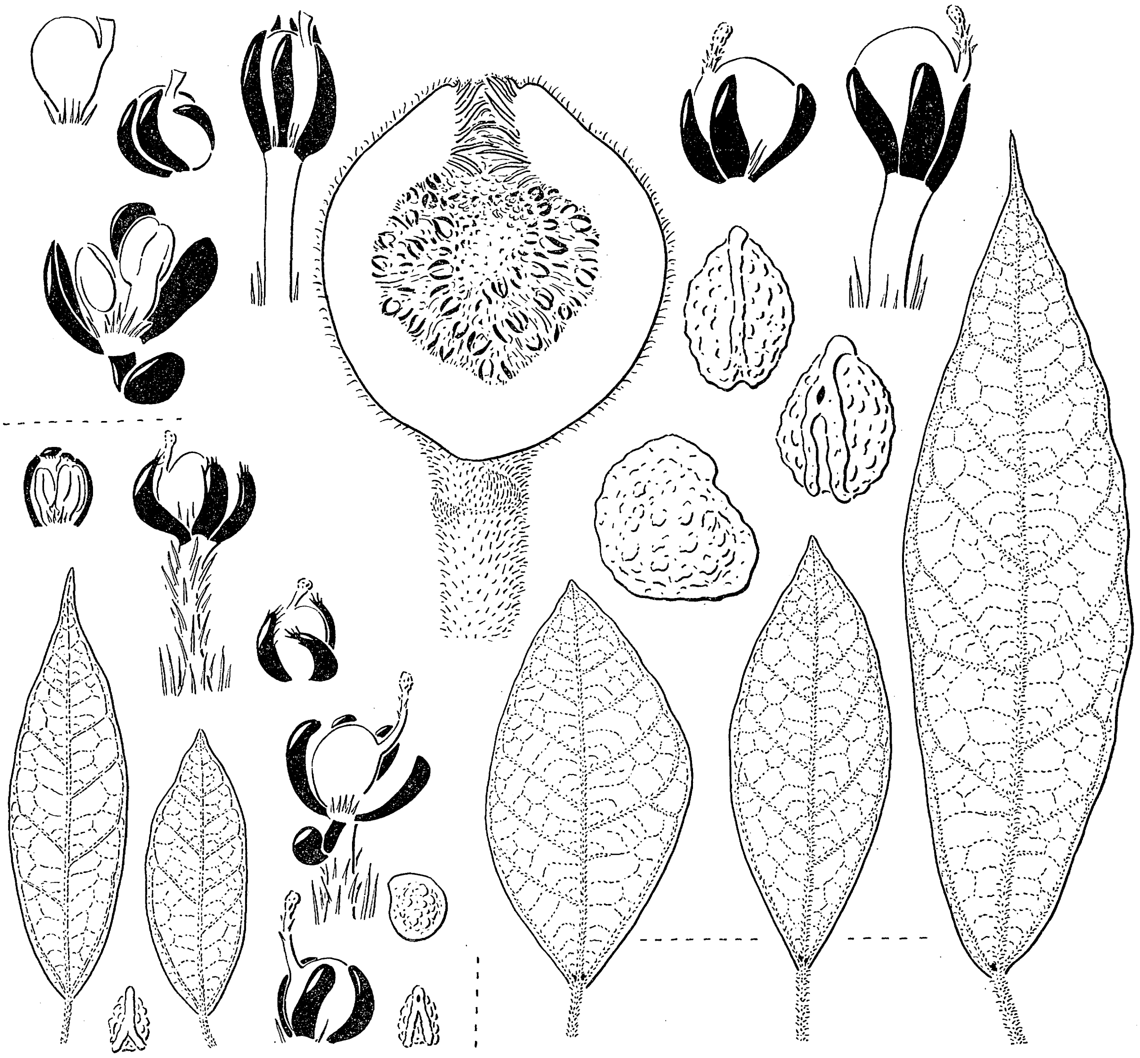

FIGURE 18. *F. litseifolia* (left) and *F. oreophila* (right); leaves, × ½; figs, × 3; flowers and seeds, × 10. Alston 14740, Forbes 2241, van Steenis 3548, *F. litseifolia*; S.F.n. 28864, Corner s.n. Fraser's Hill, *F. oreophila*.

Two points bearing on the origin of *F. carica* emerge from this discussion. Much of the ancestry of subsect. *Eriosycea* has been connected with the mountain ranges of southeast Asia and west Malaysia. Climatically, for the growth of *Ficus*, this environment joins up with the lowland and submontane regions of south China and north India. Then, from this mountain environment with abundance of landslips and seral forest, lowland species have emerged to become widespread members of the secondary forest. In Malaya, for instance, *F. aurata*, *F. chartacea*, *F. fulva* and *F. grossularioides* mix together as descendents of four stocks of the subsection and can be rated among the very common small trees of landslip, riverside and open country. This is also the relation between the three species of ser. *Cariceae*, the distribution of which has been expounded at length by Croizat (1968, pp. 274–277). *F. carica* and *F. iidaiana* (Bonin Isl.) are the subpachycaul, northerly and subtropical species, focusing the pachycaul ancestry in Sino-Himalaya. The third species is the slender *F. palmata* which has been taken to be the wild ancestor of the cultivated fig because it resembles a miniature of *F. carica*. In the light of subsect. *Eriosycea*, however, *F. palmata* is the leptocaul, tropical, lowland, widespread derivative of

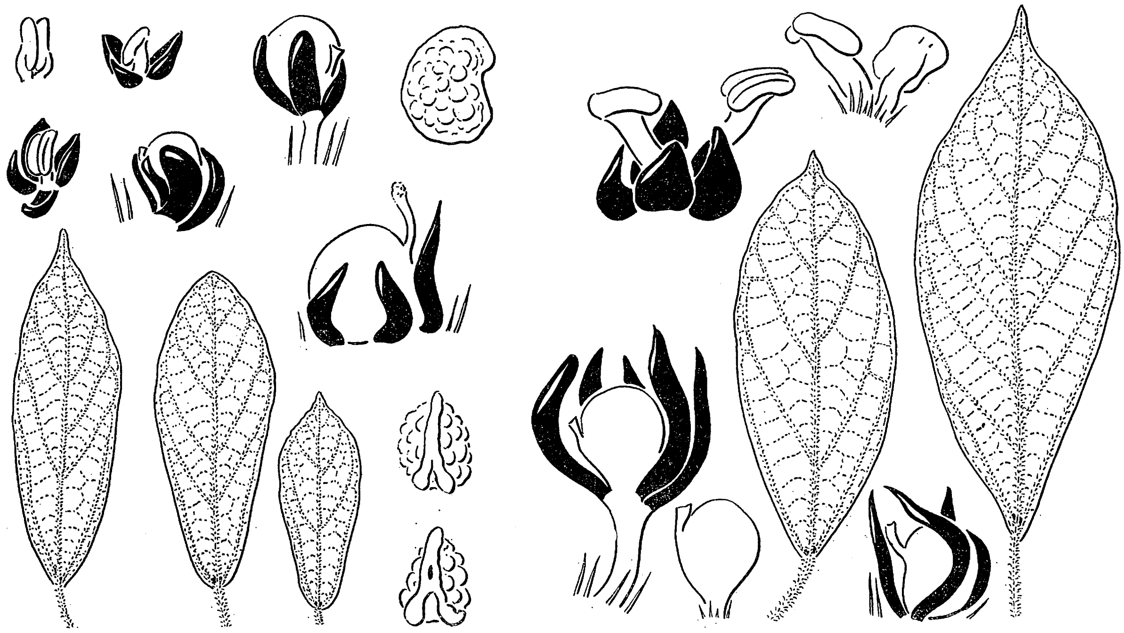

FIGURE 19. *F. tuphapensis* var. *tuphapensis* (left) and var. *annamensis* (right); leaves × ½; flowers and seeds × 10. Bon 4978, C.C.C. 9483, Henry 9908, var. *tuphapensis*; Kerr 3742, Poilane 1541, var. *annamensis*.

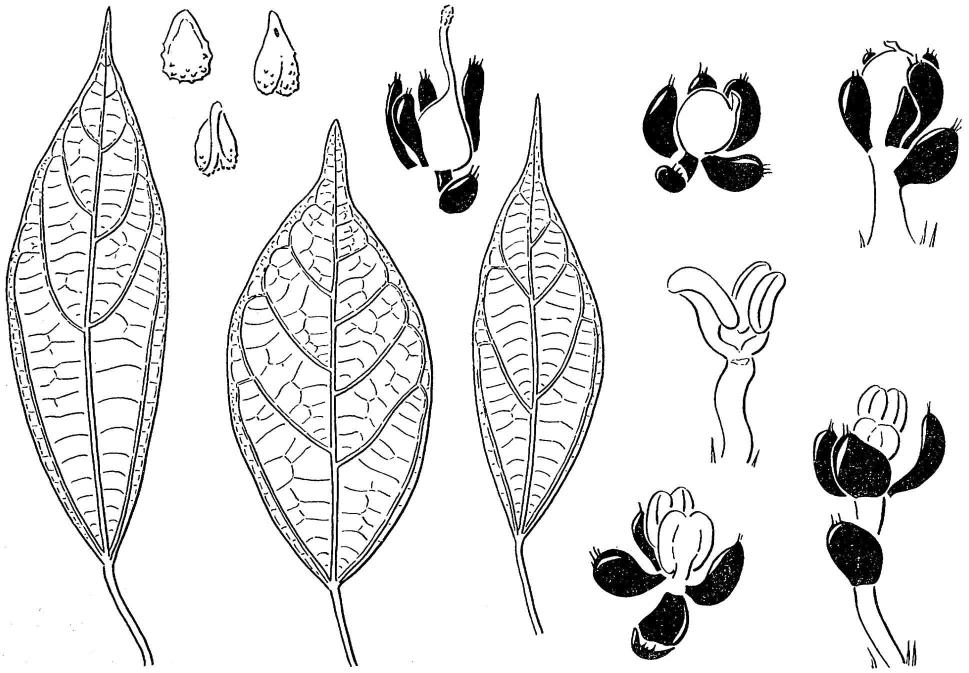

FIGURE 20. *F. langkokensis*, leaves, × ½; flowers and seeds, × 10; Balansa 2959, C.C.C. 9460, C.I.Lei 274, Poilane 7612.

the pachycaul ancestry of ser. *Cariceae*, enjoying the dry open country from India to east Africa, as *F. chartacea* is to *F. hirta* in the wet climate of Malaya. I not here what I have remarked elsewhere that *F. carica* grows vigorously in Malayan lowlands but very soon falls prey to the attacks of boring beetles which consume it, from longicorns in the root to weevils in the twigs. The failure to grow this species under such conditions gives a glimpse of one of the ecological factors determining the distribution of species of *Ficus*. I do not consider that adaptation to dry or wet climates represents vicariism any more than to lowland or mountain habitats because vicariism implies diversification from and elimination of a formerly widespread ancestor that occupied all the territory. Evolution in *Ficus* has taken the new species into new habitats which the ancestor could not achieve.

II. *F. sciaphila* sp.nov. and the pachycaul ancestry of sect. *Sycidium* ser. *Copiosae*

The dioecious and predominantly unistaminate sect. *Sycidium* is one of the advanced groups of *Ficus*. It lacks the particularities of sect. *Adenosperma* and *Sycocarpus*, and in this relative simplicity it may be an aggregation of convergent lines of evolution. In subsect. *Sycidium*, ser. *Prostratae* and *Pungentes* may be examples for they are pollinated by *Ceratosolen* and their alliance may be with sect. *Adenosperma* and *Sycocarpus*. The other three series of the subsection form botanically a natural progression from ser. *Phaeopilosae* (dark brown hairs, spirally arranged leaves) through ser. *Copiosae* (colourless hairs, spirally arranged leaves) to ser. *Scabrae* (colourless hairs, distichous leaves). So far as known they are pollinated by *Blastophaga*, but it seems that the insects of ser. *Phaeopilosae* and ser. *Copiosae* may be intermediate with *Ceratosolen* (Wiebes 1963, 1964). Geographically the three series belong to central and east Malaysia, Melanesia, Micronesia and Polynesia (Corner 1967). The only one to have a footing on the Asian mainland is ser. *Copiosae*. The question arises whether this small series of twelve species is comparable with ser. *Nervosae* of subgen. *Pharmacosycea* and runs a course of evolution from the surrounds of the Coral Sea or belongs to China Sea as with sect. *Ficus*.

The species of ser. *Copiosae* fall into two groups. Those of west Malaysia and the Asian mainland have reticulately pitted seeds. The rest in central and east Malaysia and Melanesia have smooth seeds, and among them a distinction arises in the position of the cystoliths, though it does not seem to have major importance; they are generally amphigenous, but they are hypogenous in *F. primaria* and *F. griseifolia*. I refer to my check-list for other details (Corner 1965, p. 132). In table 3 the distribution is set out with the state of pachycauly. This last feature is rendered very unsatisfactorily by the thickness of the twig in herbarium specimens. With large-leafed plants the collector avoids the massive twigs, prefers the ultimate ramifications with small leaves, even the incipient sprigs from the trunk, and neglects the stouter sapling. Ideally for every species there is needed a curve of primary stem thickness from seedling through sapling to adult and old age. This would show that *F. copiosa* stands always above *F. wassa* in stoutness.

It seems that there have been two pachycaul centres, that in southeast Asia identified through *F. andamanica* and that in Melanesia. The link may be provided by *F. balica* which occupies the Java–Timor arc and has the primitive mark of setose flower-pedicels. According to Croizat (1968, pp. 104–110), the distribution of ser. *Copiosae* follows a standard track along the Australian Foreland where the all-pervading ancestor split up vicariously at centres of diastrophism to produce the chain of modern species (Croizat 1968, f. 14, 18). This explanation does not account for the alliance with ser. *Phaeopilosae* and ser. Scabrae in Melanesia, though Croizat links these two with subgen. *Ficus* sect. *Sinosycidium* in China, chiefly because he finds the possibility of migration of modern species from the Solomons to Madagascar 'quite disturbingly imaginary'. Vicariism does not explain, also, the almost complete congruence in distribution of the two commonest species, namely *F. copiosa* (often bistaminate, subpachycaul) and *F. wassa* (unistaminate, leptocaul).

These two species differ mainly in the size of their parts (Corner 1967, f. 25). In the forest where they often grow together, they are easily distinguished, but in the herbarium sapling *wassa* can pass for adult *copiosa* and the distinction becomes difficult. The rough leaves of *F. wassa* are used locally for sandpaper; the large young leaves of *F. copiosa* are eaten as a vegetable; the two are never confused in the village. Thus both come to be well known, and the problem of the origin of the smooth-seeded species of ser. *Copiosae* has seemed to me to be linked with that of *F. copiosa*. From an inspection of their distribution and that of their allies, New Guinea and New Britain would appear to have been the source. The large tree *F. primaria* is certainly related and is limited precisely in this way. According to the theory of vicariism, however, the ancestor occupied the whole range from Burma to New Hebrides. I come now to the new facts which could not previously have been published.

TABLE 3. SPECIFIC DISTRIBUTION AND TWIG-SIZE IN SER. *COPIOSAE*

	twig diam. (mm)	An	Bu	Th	Mal	Sum	J	Bo	PI	C	Mol	NG	NB	Sol	NH	Q	
F. sciaphila	5–8	.	.	.	.	.	.	.	.	.	.	.	—	.	.	.	
F. copiosa	3–6	.	.	.	.	.	.	.	.	—	—	—	—	—	.	—	
F. wassa	2–4	.	.	.	.	.	.	.	.	.	—	—	—	—	—	.	(i)
F. hystricicarpa	2–3	.	.	.	.	.	.	.	.	.	.	—	.	.	.	.	
F. heteropoda	3–8	.	.	.	.	.	.	.	—	—	—	.	.	.	.	.	
F. subsidens	2–4	.	.	.	.	.	.	—	.	.	.	.	.	.	.	.	
F. balica	2–4	.	.	.	.	.	—	.	.	.	.	.	.	.	.	.	(ii)
F. primaria	5–6	.	.	.	.	.	.	.	.	.	.	—	—	.	.	.	
F. griseifolia	2–3	.	.	.	.	.	.	.	.	.	.	—	.	.	.	.	
F. andamanica	4–6	—	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(iii)
F. madurensis	3–5	.	—	—	—	—	—	.	.	.	.	.	.	.	.	.	
F. montana	1–3	.	—	—	—	—	—	—	.	.	.	.	.	.	.	.	

An, Andamans; Bo, Borneo; Bu, Burma; C, Celebes; J, Java; Mal, Malaya; Mol, Moluccas; NB, New Britain; NG, New Guinea; NH, New Hebrides; PI, Philipines; Q, Queensland; Sol, Solomons; Sum, Sumatra; Th, Thailand.

(i) Also Flores, Timor. (ii) East Java to Flores. (iii) Also Nicobar Isl.

I found in 1960 a small, typically pachycaul fig tree in the dense primary forest near Keravat in New Britain. It was sterile but scars on the stem showed that it had been cauliflorous. It was obviously a new species of great interest but no other plant could be found though I gathered a dozen helpers from the staff of the Forest Department and spent two days in the search. These local men, well informed about their plants, declared that this one was unknown to them. Though subsequent examination showed the presence of amphigenous cystoliths, I could not decide if the species belonged to sect. *Adenosperma*, *Sycidium* or *Sycocarpus*. One point favoured ser. *Copiosae*; it was the presence of lanceolate, persistent paired stipules over the terminal bud as in *F. copiosa* and *F. wassa*.

Eight years later I was sent a second and fertile specimen, also from the northeast end of New Britain. The figs were young and had become mouldy, and many maggots had devoured most of the flowers; yet I found sufficient to ascertain that the species, which I call *F. sciaphila*, is a bistaminate ally of *F. copiosa*. Here, then, in the territory of *F. copiosa*, *F. wassa* and

F. primaria there is the rare undergrowth prototype of the series comparable with *F. diamantiphylla* in ser. *Auratae*. These discoveries prove that the pachycaul plants are the ancestral relics which have lingered in the forest about the place where their series originated. They do not fulfil extensive tracks, as the theory of vicariism requires, but their more adaptable descendents may come to occupy these tracks so far as migration has been possible. If vicariism had operated, *F. sciaphila* or some very similar plant should be discoverable in any country within the range of the series.

If *F. sciaphila* links up the origin of ser. *Copiosae* with that of ser. *Phaeopilosae* and *Scabrae* on the Melanesian Foreland (Corner 1967,) it does not account for the western complex of *F. andamanica*. The pitted seed may have greater importance than I had imagined because it occurs also in the rather isolated *F. exasperata* of Ceylon, south India, Arabia and east Africa. I placed this species in sect. *Sycidium* subsect. *Varinga* because of the oblong seed; moreover, the shortly petiolate, distichous leaves seemed to agree with other members of this Afro–Asian complex. I must defer this problem to a later date.

F. sciaphila sp. nov. (figure 21) (Check-list no. 300 A)

A *F. copiosa* recedit ramulis crassioribus 5–8 mm latis, foliis praecipue spiraliter congestis haud muriculatis, laminis majoribus 30–50 × 11–22 cm, costis lateralibus utrinsecus pluribus 9–16, petiolis brevioribus crassioribus 10–40 × 4–5 mm, syconiis (ut videtur) ellipsoideo-oblongis (haud depresso-globosis).

New Britain; NGF 13780 (sterilis), Keravat, leg. E. J. H. Corner 14 Oct. 1960; NGF 38054, Rabaul, subdistrict Lackit, 800 m alt., leg. C. Ridsdale et P. Katik, 4 April 1968 (syconiis immaturis; typus, CGE).

Small tree 4–6 m high, with few widespread branches, cauliflorous. Leaves spirally arranged in rosettes or subdecussate. Glabrous. Twigs 5–8 mm thick, becoming hollow, light brown. Stipules 15–30 mm long, brown, scarious, longitudinally striate, caducous or subpersistent. Lamina 27–50 × 11–22 cm, obovate, acuminate with the tip 15–25 mm long, gradually narrowed to the shallowly cordate symmetric base, distantly denticulate to entire, subscabrid on both sides, membranous subcoriaceous, drying grey-green; lateral veins 9–16 pairs, strongly raised below, with axillary glands; intercostals 6–11, raised below; basal veins 3 pairs, short, or the larger somewhat elongate, with two large basal glands; petiole 15–40 × 4–5 mm, flattened, becoming woody with flaking epidermis. Figs pale purple (immature), borne on congested twigs up to 2 cm long on the trunk; stalk 35–50 × 2 mm, with 2–3 small scattered bracts 1–1.5 mm long; body 28 × 22 mm, ellipsoid, the orifice sunken; internal bristles short, white. Male flowers ostiolar; tepals 5–6 white, ciliato-dentate; stamens 2. Gall flowers more or less sessile; tepals 5, white or pinkish, ciliato-dentate; style glabrous. Cystoliths amphigenous; sphaerocrystal cells in both epidermal layers.

In dense lowland forest and on limestone.

It is to be hoped that mature gall-figs and seed-figs will be collected, along with the sapling, and that both the pollinating insects and the marauding insects will be found. Wiebes (1961, 1966) recorded the new fig-wasp genus *Grandiana* from *F. wassa*.

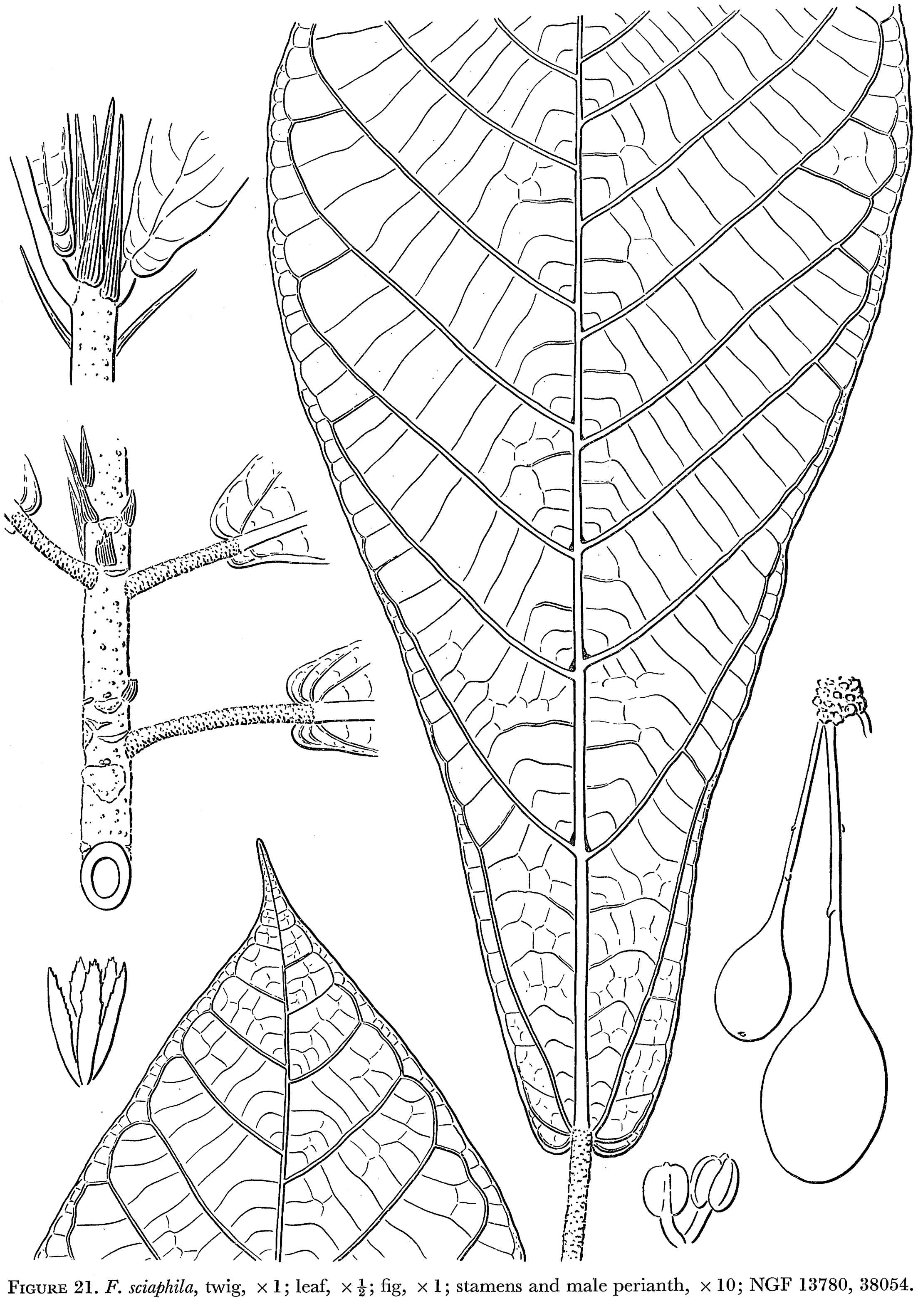

FIGURE 21. *F. sciaphila*, twig, × 1; leaf, × ½; fig, × 1; stamens and male perianth, × 10; NGF 13780, 38054.

References

Baas, P. 1969 Comparative anatomy of *Platanus kerri* Gagnep. *Bot. J. Linn. Soc.* **62**, 413–421.

Corner, E. J. H. 1960*a* Taxonomic notes on *Ficus* Linn., Asia and Australasia. III, subgen. *Ficus* and sect. *Ficus*. *Gdns' Bull. Singapore* **17**, 416–441.

Corner, E. J. H. 1960*b* Taxonomic notes on *Ficus* Linn., Asia and Australasia. IV, subgen. *Ficus* sect. *Sycidium* Miq. *Gdns' Bull. Singapore* **17**, 442–485.

Corner, E. J. H. 1962 The classification of Moraceae. *Gdns' Bull. Singapore* **19**, 187–252.

Corner, E. J. H. 1965 Check-list of *Ficus* in Asia and Australasia. *Gdns' Bull. Singapore* **21**, 1–186.

Corner, E. J. H. 1967 *Ficus* in the Solomon Islands. *Phil. Trans. Roy. Soc. Lond.* B **253**, 23–159.

Corner, E. J. H. 1969*a* The complex of *Ficus deltoidea*; a recent invasion of the Sunda Shelf. *Phil. Trans. Roy. Soc. Lond.* B **256**, 281–317.

Corner, E. J. H. 1969*b* *Ficus* sect. *Adenosperma*. *Phil. Trans. Roy. Soc. Lond.* B **256**, 318–355.

Corner, E. J. H. 1970 *Ficus* subgen. *Pharmacosycea* with reference to the species of New Caledonia. *Phil. Trans. Roy. Soc. Lond.* B. **259**, 383–433.

Croizat, L. 1968 The biography of the tropical lands and islands east of Suez-Madagascar; with particular reference to the dispersal and form-making of *Ficus* L. and different other vegetal and animal groups. *Att. Ist. bot. Lab. critt. Univ. Pavia* (Ser. 6) **4**, 3–400.

Hill, D. S. 1967 *Figs* (Ficus *spp.*) *of Hong Kong*. Hong Kong University Press.

Wiebes, J. T. 1961 Indo-Malaysian and Papuan fig wasps (*Hymenoptera, Chalcidoidea*). I. *Grandiana wassae* nov.gen., nov.spec. (Idarninae). *Nova Guinea Zool.* **14**, 245–252.

Wiebes, J. T. 1963 Taxonomy and host preferences of Indo-Australian fig-wasps of the genus *Ceratosolen* (Agaonidae). *Tijdschr. Ent.* **106**, 1–112.

Wiebes, J. T. 1964 Indo-Malayan and Papuan fig wasps. 3. Insects from *Ficus conocephalifolia*, with a note on the *Sycophaginae*. *Nova Guinea Zool.* **27**. 75–86.

Wiebes, J. T. 1966 Provisional host catalogue of fig wasps (Hymenoptera, Chalcidoidea). *Zool. Verh. Leiden* **83**, 1–44.